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PHREATIC HYDROBIIDS (GASTROPODA: PROSOBRANCHIA) FROM THE EDWARDS (BALCONES FAULT ZONE) AQUIFER REGION, SOUTH-CENTRAL TEXAS

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ABSTRACT

This paper provides a systematic analysis of phreatic hydrobiids from 23 localities in south-central Texas, including 14 artesian wells and four springs in the Edwards (Balcones Fault Zone) Aquifer. *Hauffenia micra* (Pilsbry & Ferriss) and *Horatia nugax* (Pilsbry & Ferriss) are redescribed as members of a new genus, and two additional new genera, seven new species and one new subspecies are also described (Table 2). Detailed morphological descriptions, provided for all taxa, emphasize characters of the shell, operculum, pallial cavity, digestive system, and reproductive system of both sexes. Two of the new genera are monotypic littoridinines having affinities with phreatic or epigean littoridinines from Mexico. The affinities of the third new genus, a hydrobiine which includes seven well-differentiated species, remain unclear. While all of the species are found in the Edwards (Balcones Fault Zone) Aquifer, at least four of the species are probably found in other aquifers of south-central Texas as well. With the description of seven new hydrobiid species, the rich and still poorly sampled troglobitic biota of the Edwards (Balcones Fault Zone) Aquifer now totals 39 troglobitic animal species, including four vertebrates.
Key words: Edwards (Balcones Fault Zone) Aquifer; south-central Texas; troglobitic fauna; Hydrobiidae; morphology; systematics.

INTRODUCTION

The Hydrobiidae (Gastropoda: Rissoacea) are a large family (over 100 genera and 1000 species; G. M. Davis, 1979) of dioecious, gill-breathing snails that have radiated into diverse fresh- and brackish-water habitats worldwide. Minute, unpigmented hydrobiids occupy groundwater habitats in numerous areas, with a large fauna occurring in karst regions of Europe (Vandel, 1965; Radoman, 1973), and lesser deployments occurring in North America (Morrison, 1949; Taylor, 1966), Mexico (Taylor, 1966; Hershler, 1984; 1985), Japan (Kuroda & Habe, 1958), and New Zealand (Ponder, 1966; Climo, 1974, 1977). Apart from the European deployment, little is known regarding the systematics and zoogeography of these taxa, in large part due the extremely small size (maximum shell dimension often > 2 mm) of the snails and difficulties in sampling their habitat.

One of the poorer known phreatic hydrobiid faunas is that of Texas. *Horatia nugax* (Pilsbry & Ferriss, 1906) and *Hauffenia micra* (Pilsbry & Ferriss, 1906), described from river drift shells, have long been the sole described hydrobiids considered phreatic in Texas. As the anatomy of these taxa has not been studied, it is not known whether they are congeneric with any of the European phreatic hydrobiids (i.e., *Horatia s.s.* and *Hauffenia s.s.*) that they resemble in shell features. Later collections from a cave (Reddell, 1965), spring (Taylor, 1974), stream drift (Strecker, 1935; Hubricht, 1940; Fullington, 1978; J. R. Davis, 1983), and artesian wells (Karnei, 1978; Longley, 1975, 1978, 1981) provided possible additional records for these species as well as probable new taxa, pointing to the presence of a diverse phreatic snail fauna in south-central Texas.

Most of these collections have been from areas underlain by the Edwards (Balcones Fault Zone) Aquifer (Fig. 1). While phreatic faunas are known from several aquifers in Texas (Reddell, 1965, 1967, 1970; Reddell &

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EDWARDS (Balcones Fault Zone) AQUIFER REGION

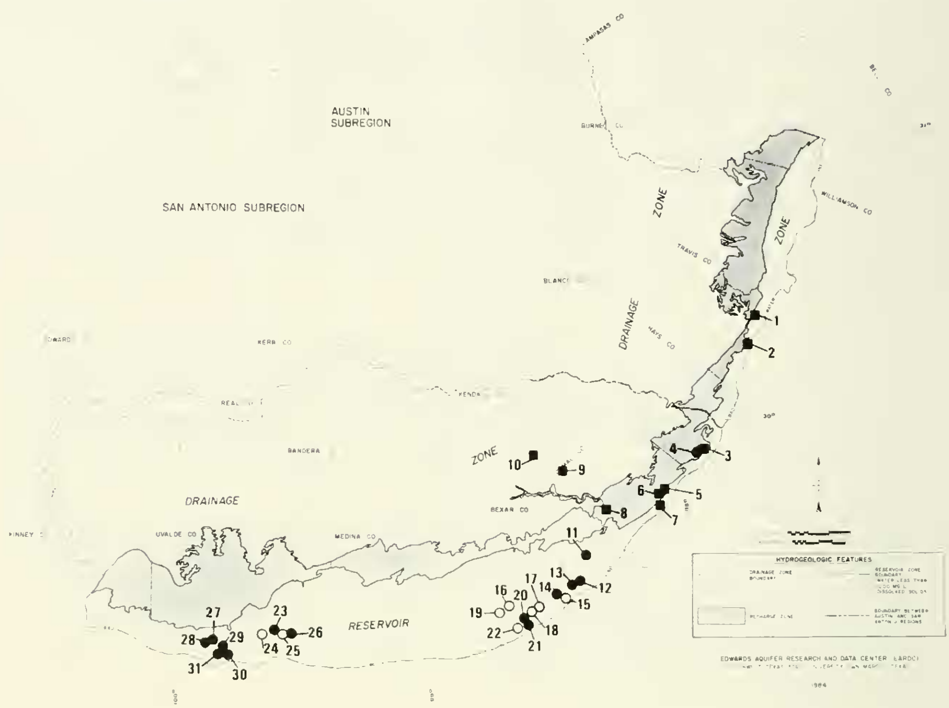

FIG. 1. Map of the Edwards (Balcones Fault Zone) Aquifer Region showing the 31 localities considered in this paper. Squares refer to springs or caves, while circles refer to artesian wells that have (filled) or have not (open) yielded hydrobiids. Locality numbers are as in Appendix 1.

Mitchell, 1969; Mitchell & Reddell, 1971), that of the Edwards is particularly rich, totalling 32 described animal species, including four vertebrates (Table 1). Twenty of these species, including nine amphipods, have been obtained from (and several are endemic to) the single well in the aquifer that has received continuous long-term sampling (Table 1), reflecting not only the high local diversity of the fauna, but also the probability that many more taxa await discovery elsewhere in the aquifer.

This diverse fauna poses a series of questions to the biologist. What are the origins of the various faunal elements? What roles have hydrologic factors such as the presence of groundwater divides played in effecting speciation in the aquifer? What is the food source for primary consumers in the deep artesian community, which has a surprisingly high trophic complexity (Longley, 1981)?

Study of the Edwards Aquifer hydrobiids is clearly necessary not only to help provide a clearer picture of this unique groundwater ecosystem, but also to further our understanding of the systematics, evolution, and adaptive radiation of the Hydrobiidae. This paper provides a systematic analysis of phreatic hydrobiids from 23 localities in south-central Texas, including 14 artesian wells and four springs in the Edwards Aquifer. We redescribe *Horatia nugax* and *Hauffenia micra* as members of a new genus and also describe two additional new genera, seven new species and one new subspecies. A classification of these taxa is given in Table 2. Detailed morphological descriptions are given for all taxa. The systematic relationships of the various taxa are assessed, with emphasis on comparisons with other phreatic hydrobiids that have been similarly studied.

The Edwards (Balcones Fault Zone) Aquifer. A brief description of the aquifer is necessary as a prelude to discussion below. For further details the reader is referred to Klemt *et al.* (1979). The Edwards (Balcones Fault Zone) Aquifer extends for 282 km (from

TABLE 1. Described biota of the Edwards Aquifer (from Reddell, 1965, 1967, 1970; Reddell & Mitchell, 1969; Longley, 1975, 1978; Bowman & Longley, 1976; Strenth, 1976; Young & Longley, 1976; Hart, 1978; Holsinger & Longley, 1980). Only troglobitic species found in the artesian zone of the aquifer are listed. Taxa marked with an asterisk have been collected from the artesian well at Southwest Texas State University.

Platyhelminthes
  Kenkiidae
    **Sphalloplana mohri* Hyman
Mollusca
  Hydrobiidae
    **Horatia nugax* (Pilsbry & Ferriss)
    Hauffenia micra (Pilsbry & Ferriss)
Arthropoda
  Cypridae
    **Cypridopsis vidua obesa* Brady & Robertson
  Cyclopidae
    **Cyclops cavernarum* Ulrich
    **Cyclops learii* Ulrich
    Cyclops varicans rebellus Lilljeborg
  Entocytheridae
    Sphaeromicola moria Hart
  Asellidae
    **Lirceolus smithi* (Ulrich)
    Asellus pilus Steeves
    Asellus redelli Steeves
  Cirolanidae
    **Cirolanides texensis* Benedict
  Monodellidae
    **Monodella texana* Maguire
  Crangonyctidae
    **Stygobromus flagellatus* (Benedict)
    **Stygobromus russelli* (Holsinger)
    Stygobromus pecki (Holsinger)
    Stygobromus balconis (Hubricht)
    Stygobromus bifurcatus (Holsinger)
  Hadziidae
    **Texiweckelia texensis* (Holsinger)
    **Texiweckelia insolita* Holsinger
    **Texiweckelia samacos* Holsinger
    **Allotexiweckelia hirsuta* Holsinger
  Bogidiellidae
    **Parabogidiella americana* Holsinger
  Artesiidae
    **Artesia subterranea* Holsinger
  Sebidae
    **Seborgia relicta* Holsinger
  Palaemonidae
    **Palaemonetes antrorum* Benedict
    Palaemonetes holthuisi Strenth
  Dytiscidae
    **Hadeoporus texanus* Young & Longley
Chordata
  Ambystomidae
    **Typhlomolge rathbuni* Stejneger
    Typhlomolge robusta Longley
  Ictaluridae
    Satan eurystomus Hubbs & Bailey
    Trogloglanis pattersoni Eigenmann

Brackettville to north of Georgetown), paralleling the Balcones Escarpment and Fault Zone in south-central Texas, and varies in width from eight to 48 km (Fig. 1). The aquifer consists of a recharge and artesian (reservoir) zone. Recharge to the aquifer occurs largely by downward percolation from streams crossing areas where the Edwards outcrops (Fig. 1). To the south and east of the recharge zone the Edwards Formation dips downward (assuming artesian conditions), and the top of the formation is as much as 600 m beneath ground level in Bexar County (Klemt *et al.*, 1979). The Cretaceous Edwards limestone that comprises the aquifer is highly porous, due to the effects of solution and faulting. The aquifer is thought to have extensive water-filled caves and caverns (Pettit & George, 1956; Klemt *et al.*, 1979). Note that the Balcones Fault Zone has the highest density of caves of any physiographic region in Texas (Smith, 1971). As a result of this high secondary porosity, transmissivity is high in the aquifer, as seen in the occurrence of a large number of high capacity wells, some of which flow at ground level and discharge several thousand liters/second (Maclay & Small, 1976; Klemt *et al.*, 1979). Several groundwater divides are present in the aquifer, and smaller phreatic pools are also thought to have resulted from the intensive folding and fracturing in the bedrock (Holsinger & Longley, 1980). South and south-east of the "bad-water" line (reservoir boundary, Fig. 1), the Edwards water has sluggish circulation and is no longer of good quality, having $>$ 1000 mg/1 total dissolved solids (Klemt *et al.*, 1979). Natural discharge of the aquifer occurs (or has occurred) at major springs near Uvalde (Leona Springs), San Antonio (San Pedro,

TABLE 2. Classification of phreatic hydrobiids from the Edwards (Balcones Fault Zone) Aquifer Region.

Family Hydrobiidae
  Subfamily Hydrobiinae
    Phreatodrobia micra (Pilsbry & Ferriss) n. gen.
    Phreatodrobia nugax nugax (Pilsbry & Ferriss)
    Phreatodrobia nugax inclinata n. subsp.
    Phreatodrobia rotunda n. sp.
    Phreatodrobia conica n. sp.
    Phreatodrobia plana n. sp.
    Phreatodrobia imitata n. sp.
    Phreatodrobia punctata n. sp.
  Subfamily Littoridininae
    Balconorbis uvaldensis n. gen., n. sp.
    Stygopyrgus bartonesus n. gen., n. sp.

San Antonio Springs), New Braunfels (Comal Springs), San Marcos (San Marcos Springs) and Austin (Barton Springs). Artificial discharge has also occurred in recent years through the hundreds of high capacity wells in the artesian zone. The Edwards (Balcones Fault Zone) Aquifer is separated from the Edwards (Plateau) Aquifer by a region where outcropped Edwards limestone has largely been eroded.

MATERIALS AND METHODS

Sampling and localities. The bulk of the material examined during this study was obtained by the well sampling program conducted by staff of the Edwards Aquifer Research and Data Center (EARDC) during 1976–1981. A total of 22 wells in the Edwards Aquifer were sampled often enough to either obtain troglobitic organisms or provide confidence that troglobites were absent in that area. Details for these wells regarding United States Geological Survey or Texas Board of Water Engineers well number, well owner, well depth, number of samples taken, and presence-absence of troglobitic fauna are given in Table 3.

Fine-mesh funnel (constricted or open) nets were attached to pipes from artesian wells using hose clamps (Fig. 2A). The collecting vessel at the end of the net was usually a 3.8 liter plastic jar, although occasionally a small section of 64 μm mesh netting material clamped to a section of polyvinylchloride (PVC) pipe (with screw-on cap) was used instead. All material collected was washed through netting attached to a plastic funnel and then transferred to 70% EtOH.

Groundwater outlets of four springs were sampled as follows. The "Pipe" (or "Diversion") orifice was sampled at San Marcos Springs. Developers of the spring capped this orifice (one of many feeding this spring) by cementing an old diving bell to the spring floor. A 29" culvert pipe was then attached to the opening of the bell to divert the spring flow elsewhere. A 29" diameter sampling net was placed at the end of the pipe to filter the water stream. At Barton Springs, sampling was done at the "Concession" Spring (Fig. 2B), which has been cemented over with several holes serving to release the spring flow.

TABLE 3. Data regarding 22 Edwards Aquifer wells that have been sampled.

Well no.	Owner	Depth (m)	Number of samples	Troglobites (+/−)
—	Southwest Texas State University	59	500+	+
AY-68-29-923	Longhorn Portland Cement Co. (#2)	143	36	+
AY-68-37-127	Brackenridge Zoo	124	45	+
AY-68-37-508	City Water Board (San Antonio) Artesian Station, Well 4	402	48	+
AY-68-36-918	Union Stockyards (#3)	412	8	+
AY-68-37-710	City Water Board (San Antonio) Mission Station	460	9	+
AY-68-43-115	J. H. Uptmore (#5)	227	10	+
AY-68-44-107	Lakeland City Water Co.	555	5	−
AY-68-44-215	City (Antonio) Public Service Board (#1)	358	22	+
AY-68-43-107	Rio Vista Farms	—	9	−
AY-68-43-608	Verstraeten Brothers	513	10+	+
AY-68-43-601	O. R. Mitchell	582	10+	+
AY-68-43-505	J. W. Watts	610	2	−
YP-69-43-103	King Farms	—	3	+
YP-69-43-801	D. C. Carnes	—	5	−
YP-69-50-? (=H-6-24)	C. Reagan	386	4	+
H-6-43	W. C. Reagan	373	5+	+
YP-69-50-109	R. Carnes	320	2	+
YP-69-50-105	R. K. Dunbar	288	2	+
H-5-135	S. Moerbe	98	2	+
H-5-158	G. Ligocky	286	10+	+
YP-69-50-501	Uvalde National Fish Hatchery	—	2	+

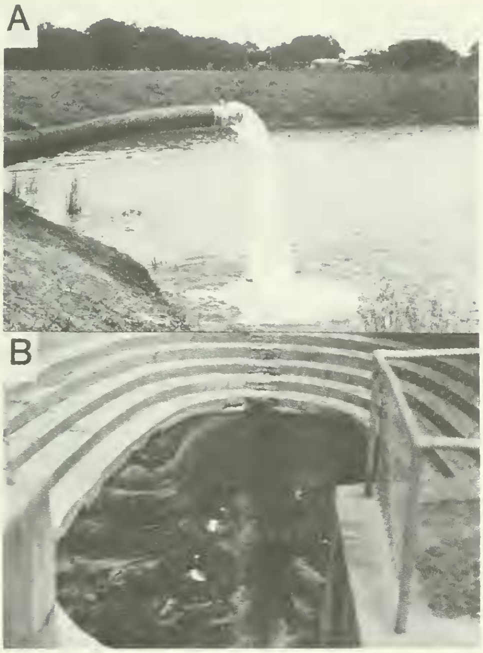

FIG. 2. Sampling nets placed on outlets of the G. Ligocky Well, Uvalde County (A) and Barton ("Concession") Springs, Travis County (B).

Three- and six-inch PVC pipes with attached irrigation "socks" or funnel netting (and "cap" type collection vessel) were wedged into these holes to sample the water stream. Similar techniques were used to sample the natural orifices at Comal (main spring) and Hueco Springs ("A", smaller; and "B", larger spring). Samples from springs were processed as above. Most of the wells and springs were sampled every 2–7 days during the sampling period.

Samples from caves were obtained by visual search for shells near permanent water and by sieving sediment with a fine hand sieve. Living snails were not obtained from any of these caves.

The location of the 31 localities considered in this paper are given in Fig. 1. Note that three of the localities (all caves) sampled are from areas not underlain by the Edwards (Balcones Fault Zone) Aquifer (see below). Locality data are given in Appendix 1.

Morphological study. Methods of morphological study largely follow those of G. M. Davis (1979) and Hershler (1985). Live material was available only for two species. Anatomical study centered on the pallial cavity (and contained structures), digestive system, and reproductive systems of both sexes. Usage of body surface references (left, right, dorsal, ventral) follows that of Fretter & Graham (1962). The nervous system was studied only in one species. Measurements of the length and width of the intestine coil in the pallial cavity refer to the maximum dimensions of the coil parallel and perpendicular to the length of the pallial cavity. To prepare snails for dissection, the calcified portion of the shell was first removed by placing individuals into concentrated Bouin's solution for 24 hours. Dissections were done using a Zeiss dissecting microscope (50X) fitted with an ocular micrometer, with specimens immersed in dilute Bouin's solution. Shells were measured using the same microscope (32X, 50X). Radulae were photographed using a scanning electron microscope. All radular data were obtained from these photographs. Shells were photographed using either a 35 mm camera attached to a Zeiss microscope, or the scanning electron microscope.

Deposition of type material. Holotypes and paratypes are deposited in the Academy of Natural Sciences of Philadelphia. Reference is made to catalog numbers (ANSP) assigned to this material. All other material examined is housed in the EARDC collection.

Taxonomic procedure. The higher level classification of the Hydrobiidae is currently confused, due to the high incidence of convergence and mosaic evolution within the family, and several classifications have recently been proposed (Taylor, 1966; Radoman, 1973; G. M. Davis *et al.*, 1982). Convergence in shell features is well documented in the Hydrobiidae (G. M. Davis, 1979) and higher-level classifications largely based on these features (i.e., Taylor, 1966) are likely to produce polyphyletic and artificial groupings. In this paper we follow the subfamilial breakdown used by G. M. Davis *et al.* (1982) in which the Hydrobiinae, Lithoglyphinae (see also Thompson, 1984), Littoridininae (see also Hershler, 1985), and Nymphophilinae are recognized. Note, however, that convergence may extend to key characters used in this classification: a spermathecal duct, diagnostic of the Littoridininae (G. M. Davis *et al.*, 1983), has apparently arisen numerous times among various rissoacean clades (Ponder, 1984). Further confusion has been added by the recent discovery of a genus having a hydrobiine-type fe-

TABLE 4. Generalized cusp formulae for the four radular tooth types.

Species	Central	Lateral	Inner marginal	Outer marginal
Phreatodrobia micra	5-1-5 / 1-1	5-1-6	21–23	13–16
Phreatodrobia nugax	5(6-8)-1-5(6,7) / 1(2)-1	5-1-6(7,8)	24–34	19–26
Phreatodrobia rotunda	6-1-5(6) / 1-1	5-1-5(6)	20–23	?
Phreatodrobia conica	6(7,8)-1-6(7,8)	7(8)-1-10(11)	21–26	15–17
Phreatodrobia plana	6(8)-1-6(7,8)	8(9)-1-11(12)	23	24–28
Phreatodrobia imitata	7(8)-1-7(8)	6(7)-1-6(7)	21–23	14–17
Phreatodrobia punctata	7(9)-1-7(8)	7(8,9)-1-10(11,12)	23–26	22–24
Stygopyrgus bartonensus	4(5)-1-4(5) / 1-1	4(5-7)-1-5(6)	22–25	15–17
Balconorbis uvaldensis	5(6)-1-4(5) / 1-1	6-1-6(7,8)	21–24	17–20

male reproductive system and a littoridinine-type penial gland (Giusti & Bodon, 1984; fig. 2B, G). While a search for morphological characters that identify clades within the Hydrobiidae must obviously be continued, we feel that the above classification is still the best available.

Only character-states unique to or diagnostic of the taxa concerned are emphasized in this paper. Radular data are presented in Table 4. Shell and other morphological data are presented in Appendices 2 and 3, respectively. The phenogram shown in Fig. 28 was generated using the CLUSTAN software package (developed by David Wishart of the Universities of St. Andrews and London), with Ward's method (error sum of squares) of clustering selected.

DESCRIPTION OF TAXA

Family HYDROBIIDAE
Subfamily Hydrobiinae
Phreatodrobia Hershler & Longley, new genus

Horatia Bourguignat, 1887 (in part): 47.
Hauffenia Pollonera, 1898 (in part): 3.

DIAGNOSIS. Shell (Figs. 3–6) minute (maximum dimension, < 2.5 mm), with four or fewer whorls, colorless, transparent, varying in shape from planispiral to trochoid to conical. Protoconch (Figs. 3K, L, S, 6F, 7A–F) with pitted microsculpture; teleoconch sculpture variable (Figs. 3–6, 8). Aperture slightly to highly flared. Operculum (Figs. 9, 10) nucleus typically sub-central; ventral surface smooth or with a central, knob-like process. Animal unpigmented and without eyespots (Figs. 11, 12). Pallial cavity typically slightly longer than wide; ctenidium absent, incomplete, or fully formed (Fig. 13A–G). Stomach chambers poorly distinguishable externally (Fig. 18). Intestine with loop(s) in roof of posterior portion of pallial cavity (Figs. 12, 13A–G), and sometimes on style sac (Fig. 18B, C). Central cusp of central and lateral teeth sometimes not enlarged relative to rest of cusp row (Figs. 16A–C, 17A–D); central teeth with (Figs. 14, 15A–E) or without (Figs. 15F–H, 16, 17A–D) basal cusps (projecting from the lateral angles). Radular cusps dagger-like in shape, sometimes highly numerous on central and lateral teeth. Pallial portion of prostate typically 50% of total prostate length (Figs. 19D, E). Penis simple, without lobes or specialized glands (Figs. 19A, C). Capsule gland usually large compared to albumen gland, with anterior end sometimes having a terminal bend or coil (Fig. 20A, B, H). Bursa copulatrix large relative to the seminal receptacle, with a straight or coiled duct, and largely or totally posterior to the albumen gland (Figs. 20, 21). Seminal receptacle and oviduct coil appressed to, or largely or totally posterior to albumen gland. Oviduct opens into the posterior or anterior end of the albumen gland.

FIG. 3. Shells of *Phreatodrobia nugax inclinata* (A–E, I)(Locality 11) and *P. micra* (F–H, J–L, M–T). Shell widths are as follows: A, B (1.33 mm, holotype); C (1.05 mm), D (1.04 mm), E (1.15 mm); F (1.10 mm), J (1.10 mm), N (1.16 mm) (syntypes, Locality 6); G (1.14 mm), K (0.945 mm), O (1.23 mm)(Locality 5A); H (0.8 mm), L (1.80 mm), P. (0.76 mm)(Locality 3); M (0.93 mm), Q (0.75 mm)(Locality 9); R (1.07 mm), S (0.89 mm), T (0.877 mm)(Locality 10). The scale bar next to I equals 0.1 mm.

REMARKS. The following features are also typical of the genus: a) the anus is positioned close to the mantle edge (Fig. 13); b) the kidney opening (Ro, Fig. 13A) is simple; c) the penis is three-four times as long as the snout (in preserved specimens), slender, with folds along the inner curvature, and coils on the right side of the "neck"; d) the gonads are simple and without lobes, and e) the anterior vas deferens exits from the mid-prostate just anterior to the end of the pallial cavity (Fig. 19D). *Phreatodrobia* is distinguished from *Horatia s.s.*, *Hauffenia s.s.*, and other European phreatic hydrobiines by its minute, fragile shell and simple penis, which lacks lobes and glandular swellings (see below). The minute shell with pitted apical microsculpture, simple penis, and lack of eyespots and body pigment distinguish *Phreatodrobia* from all other described North American hydrobiids. Apart from these features, the following shared character-states unite the morphologically diverse members of this genus: operculum nucleus central or near-central; pallial prostate relatively large; intestine with loop(s) in pallial roof; and bursa large relative to seminal receptacle and positioned partly or totally posterior to the albumen gland.

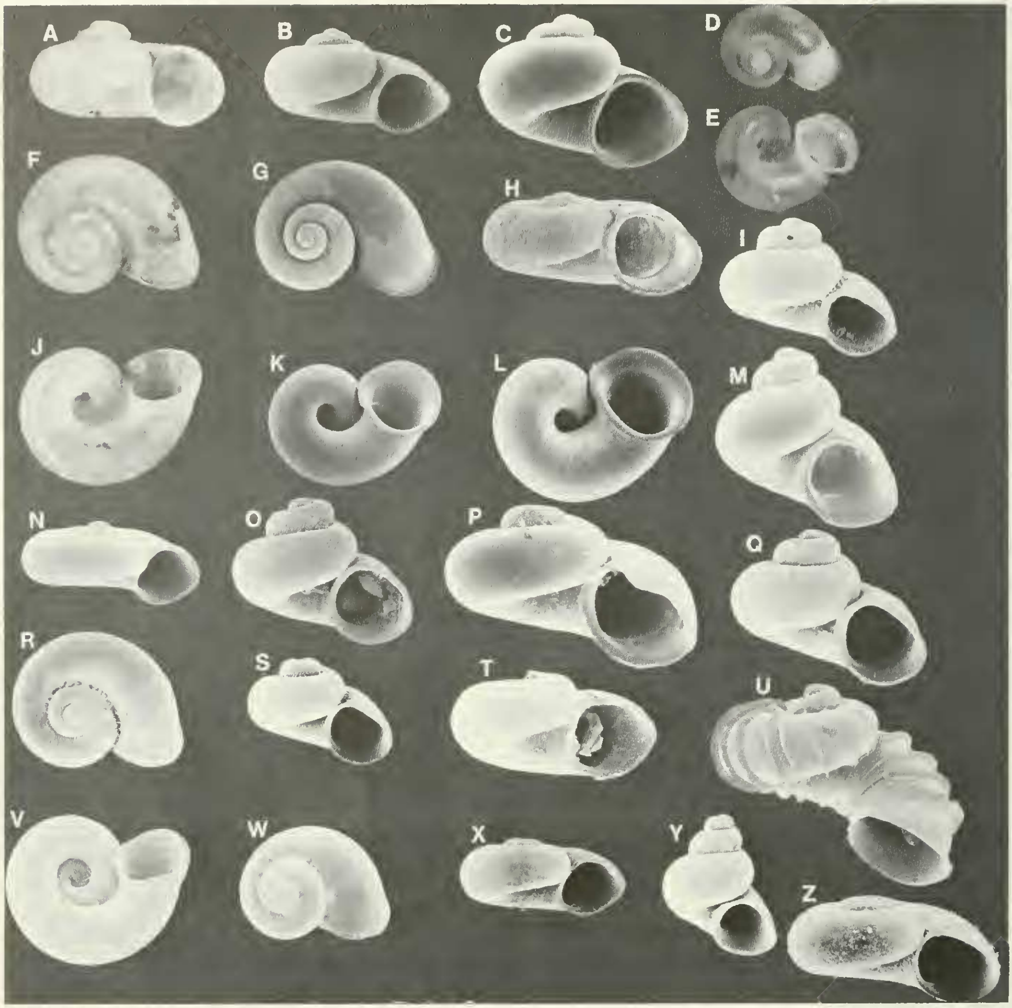

FIG. 4. Shells of *Phreatodrobia nugax nugax*. Shell widths are as follows: A, F, J (1.23 mm, holotype, Locality 6); B (1.71 mm), G (1.71 mm), K (1.6 mm)(Locality 4); C (1.55 mm), D (1.79 mm), E (1.79 mm), H (1.23 mm), L (1.53 mm)(Locality 3); I (1.07 mm, Locality 1); M (1.0 mm), Q (1.13 mm), U (1.47 mm), Y (1.09 mm), Z (0.89 mm)(Locality 2); N (1.57 mm), R (1.51 mm), V (1.64 mm)(Locality 8); O (1.53 mm)(Locality 10); P (1.08 mm)(Locality 24); S (0.85 mm), W (0.85 mm)(Localtiy 9); T (0.85 mm)(Locality 12); X (0.945 mm)(Locality 14).

TYPE-SPECIES. *Phreatodrobia micra* (Pilsbry & Ferriss, 1906).

DISTRIBUTION. Found throughout the Edwards (Balcones Fault Zone) Aquifer. Some species also probably live in other aquifers in south-central Texas (see below).

ETYMOLOGY. The generic name is derived from the Greek word *phreatos*, referring to the groundwater habitat shared by members of this taxon.

Phreatodrobia micra (Pilsbry & Ferriss)
Figs. 3F–H, J–T, 9F, G, 13B, 15A–C, 20D

Valvata micra Pilsbry & Ferriss, 1906: 172–173.

Horatia (Hauffenia) micra (Pilsbry & Ferriss). Pilsbry, 1916: 84

Hauffenia micra (Pilsbry & Ferriss). Burch, 1982: 30.

MATERIAL EXAMINED. HAYS COUNTY: San

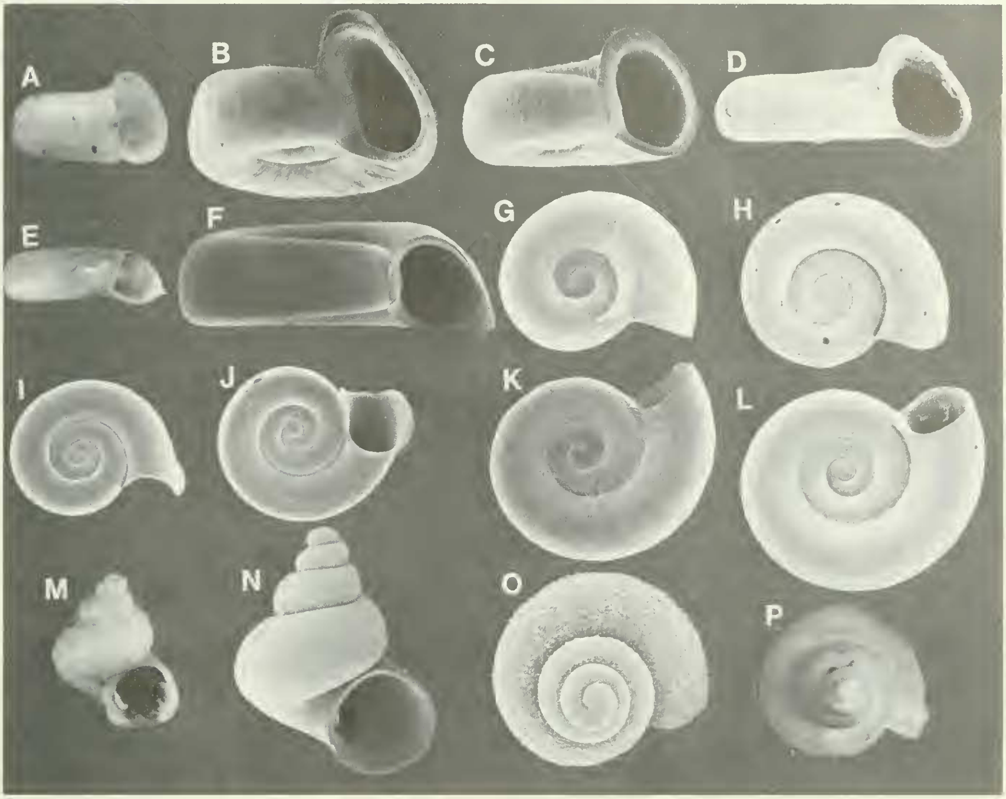

FIG. 5. Shells of *Phreatodrobia plana* (A–D, G, H, K, L), *P. rotunda* (E, F, I, J; Locality 3), and *P. conica* (M–P). Shell widths are as follows: A (0.822 mm, holotype), B (0.830 mm), C (0.77 mm), G (0.64 mm), K (0.74 mm)(Locality 3); D (1.14 mm), H (0.945 mm), L (1.12 mm)(Locality 8); E (2.26 mm, holotype, ANSP), F (1.99 mm), I (1.84 mm), J (2.06 mm); M (shell height, 1.61 mm, holotype, ANSP), N (shell height, 1.79 mm), O (1.29 mm)(Locality 5B); P (0.945 mm; Locality 5A).

Marcos Springs. COMAL COUNTY: Guadalupe River drift; Honey Creek Cave; Hueco Springs. KENDALL COUNTY: Century Caverns.

DIAGNOSIS. A small-sized species (shell width about 1.00 mm) with a planispiral, or near-planispiral shell, and a circular aperture that abuts against the penultimate whorl (Figs. 3F–H, J–T). Operculum (Figs. 9F, G) circular, with well-developed knob-like process on ventral surface; nucleus central. Ctenidium incomplete; osphradium fills large (39%) fraction of pallial cavity length (Fig. 13B). Central tooth of radula with single pair of basal cusps (Fig. 15C). Stomach almost twice as long as style sac; intestine with tight, U-shaped loop in pallial roof; long axis of loop at oblique angle to pallial cavity length (Fig. 13B). Ovary and testis occupy large proportion (50%) of digestive gland length. Albumen and capsule glands about equal in length (Fig. 20D). Oviduct opens into anterior end of albumen gland.

REMARKS. Distinctive features of this species include the typically planispiral shell with tubular whorls and simple aperture, circular operculum with well-developed process on the ventral surface, incomplete ctenidium, large-sized osphradium, and large-sized ovary and testis.

DESCRIPTION. The shell has 2.2–2.5 tubular whorls and averages 0.84–1.08 mm in width for the four populations studied. The protoconch has 1.25 whorls and has fairly

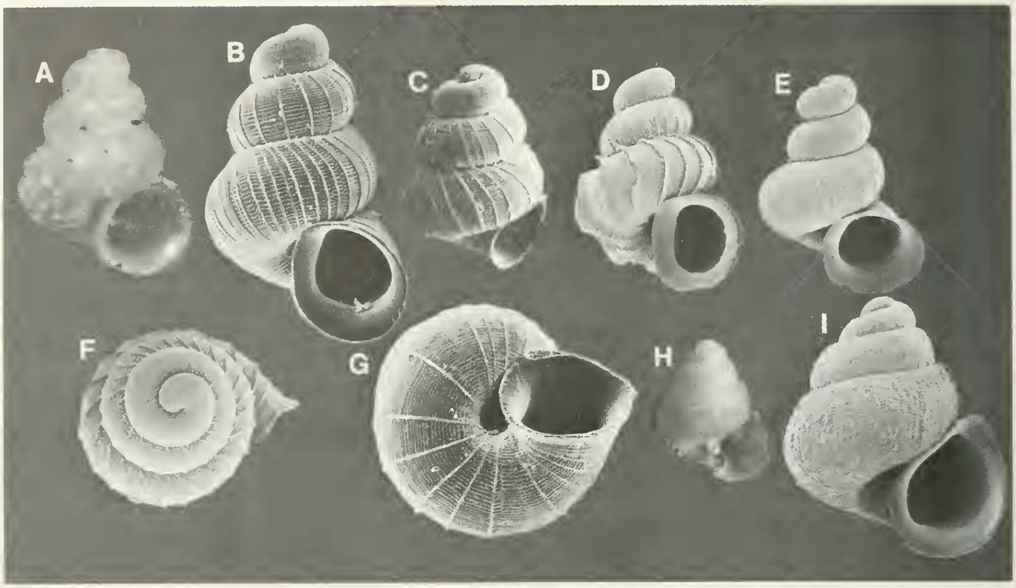

FIG. 6. Shells of *Phreatodrobia imitata* (A–G) and *P. punctata* (H, I; Locality 3). Shell heights are as follows: A (1.07 mm, holotype), B (1.05 mm), C (0.89 mm), D (1.05 mm), F (shell width, 0.75 mm), G (shell width, 0.75 mm)(Locality 20); E (1.0 mm; Locality 21); H (1.05 mm, holotype), I (1.15 mm).

large and deep pits (Fig. 3K, L, S). Axial growth lines are weakly developed on the teleoconch. Only the sample from Century Caverns includes shells with a slight spire projecting above the coil of the body whorl (Fig. 3R). A slight flaring of the aperture, particularly the inner lip, is seen in some specimens. The aperture is never free from the body whorl.

The description of operculum and anatomy is based on study of specimens from San Marcos Springs. The flat, thickened operculum has 2.5 whorls and is dark amber in color. The elevated knob-like process occupies a small portion of the operculum area and is composed of horny material (as is the rest of the operculum).

All specimens dissected had an incomplete ctenidium, consisting of an efferent branchial vessel (Ev) with a few stubby filaments at its anterior end (Fig. 13B). The filaments are much smaller, relative to pallial cavity width, than those of *Phreatodrobia nugax* (see below). A similar incomplete ctenidium was described for *Paluccia* Giusti & Pezzoli, a European hydrobiid (Giusti & Pezzoli, 1981). The large osphradium is typically positioned towards the anterior end of the incompletectenidium (Fig. 13B).

The central tooth of the radula is trapezoidal in shape. Note that the lateral angles are highly divergent (Fig. 15C). The stomach lacks a caecal appendix.

The ovary and testis consist of a solid, non-lobed mass. The vas deferens exits from the anterior end of the testis and consists of a few thickened coils (as in Fig. 18C) on the posterior half of the stomach. The prostate overlies the entire style sac and its anteriormost 44% is pallial. The penis is three-four times as long as the snout. The capsule gland opening is wide and slightly subterminal. The anterior portion of the capsule gland lacks a twist or coil. The tight coil of the anterior oviduct is appressed to the albumen gland and the seminal receptacle opens into the left side of the coil (Fig. 20D). The oviduct enters the albumen gland just after receiving the short duct from the bursa copulatrix.

HOLOTYPE. ANSP 91322 (cotypes) (Fig. 3F, J, N).

TYPE-LOCALITY. Drift debris of Guadalupe River about four miles above New Braunfels, Comal County (Fig. 1, Locality 6).

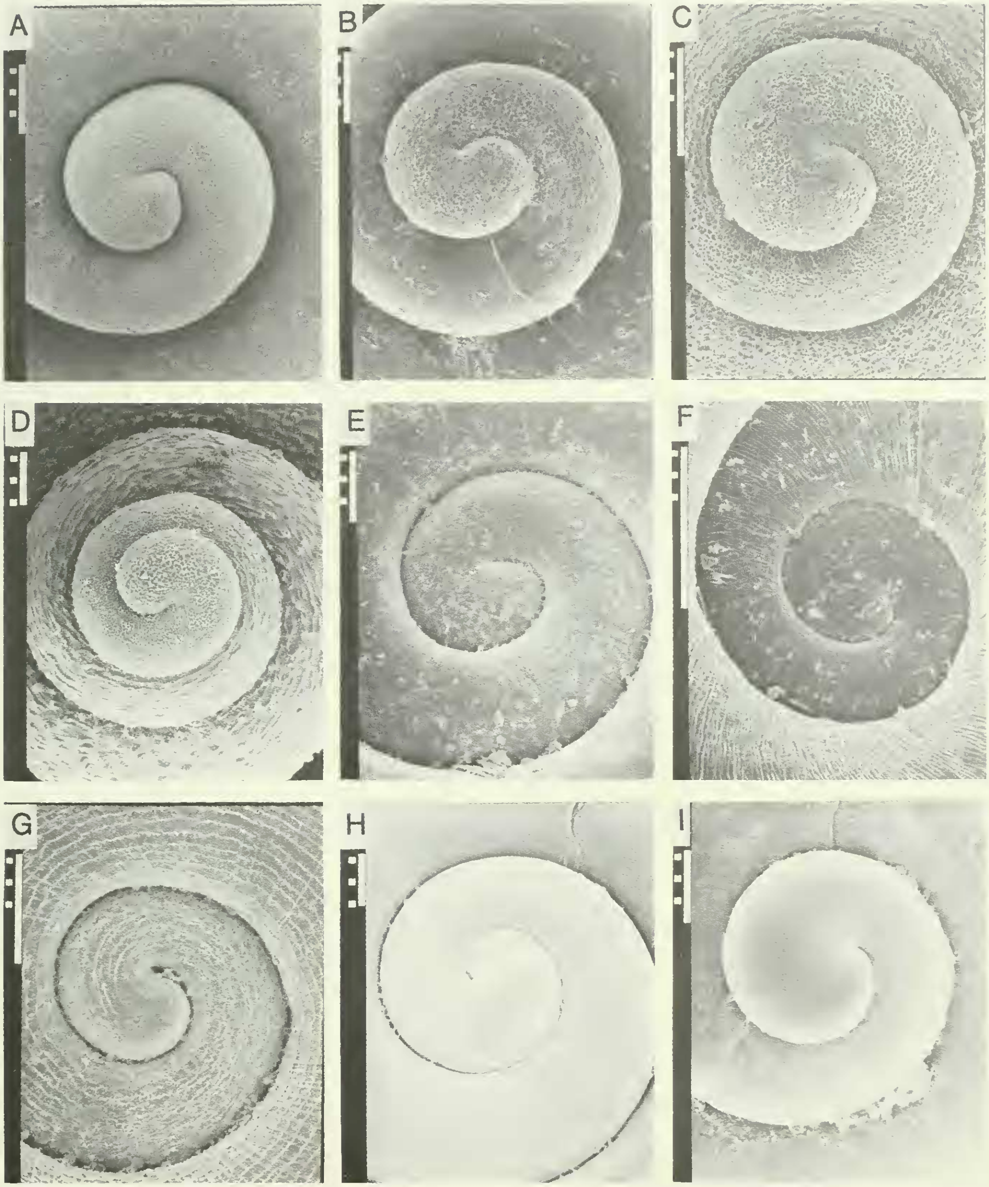

FIG. 7. Protoconchs of *Phreatodrobia nugax nugax* (A, B; Localities 3, 2), *P. punctata* (C, Locality 3), *P. conica* (D, Locality 5B), *P. rotunda* (E, Locality 3), *P. plana* (F, Locality 3), *Balconorbis uvaldensis* (G, Locality 30), "*Horatia*" sp. (H), and *Hauffenia subpiscinalis* (I). All scale bars equal 0.1 mm.

DISTRIBUTION. Edwards (Balcones Fault Zone) Aquifer, and (possibly) Cow Creek and Glen Rose Aquifers in Hays, Comal, and Kendall Counties (Fig. 1, Localities 3, 5, 6, 9, 10).

Phreatodrobia nugax (Pilsbry & Ferriss)
Figs. 3A–E, I, 4, 7A, B, 9A–E, 10–12, 13A, 14, 18A, 19A, B, D

Valvata micra nugax Pilsbry & Ferriss, 1906:

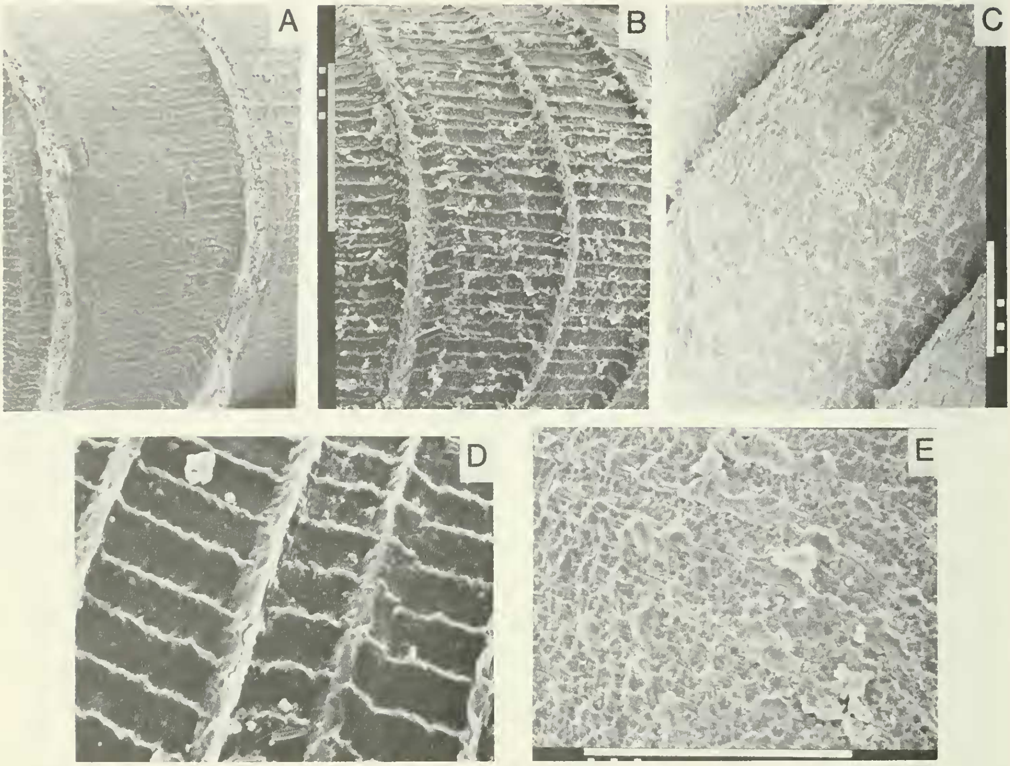

FIG. 8. SEM photographs of shell sculpture on *Phreatodrobia imitata* (A, B, D; Locality 20), *P. conica* (C; Locality 5B), and *P. punctata* shells (E, Locality 3). All scale bars equal 0.1 mm. The distance between spiral lines in D is 0.01 mm.

173.

Horatia (Hauffenia) micra nugax (Pilsbry & Ferriss). Pilsbry, 1916: 84.

Horatia nugax (Pilsbry & Ferriss). Taylor, 1975: 131.

MATERIAL EXAMINED. TRAVIS COUNTY: Salamander Cave; Barton Springs. HAYS COUNTY: San Marcos Springs; SWTSU Well. COMAL COUNTY: Guadalupe River drift; Natural Bridge Caverns; Honey Creek Cave. KENDALL COUNTY: Century Caverns. BEXAR COUNTY: Longhorn Portland Cement Company Well; Brackenridge Zoo Well; Union Stockyards Well. UVALDE COUNTY: W. C. Reagan Well.

DIAGNOSIS. A moderately large species (shell width about 1.3 mm), typically with a low trochoid shell (Figs. 3A–D, 4), but varying from near planispiral (Fig. 4H, N, X, Z) to low conical (Fig. 4Y). Aperture often free from penultimate whorl and highly flared; last 12% of body whorl highly thickened, imparting a white, opaque appearance to this part of shell (Fig. 4D, E). Operculum can have a central elevated thickening (Fig. 9B, D) on ventral surface. Ctenidium complete, with eight to 18 low filaments; osphradium length typically 25% of that of the pallial cavity (Fig. 13A). Central radular tooth with one or two basal cusps (Fig. 14). Stomach length almost twice that of the style sac (Fig. 18A); intestine with loose U-shaped loop in pallial roof; long axis of loop at oblique angle to pallial cavity length (Fig. 13A). Ovary and testis occupy large proportion (67%, 57%) of digestive gland length. Capsule gland with (Fig. 20A, B) or without terminal coil; oviduct opens into anterior end of albumen gland.

REMARKS. This species is distinguished by its low trochoid shell with thickened end of body whorl, complete ctenidium, and unusually large ovary. The capsule gland coil and

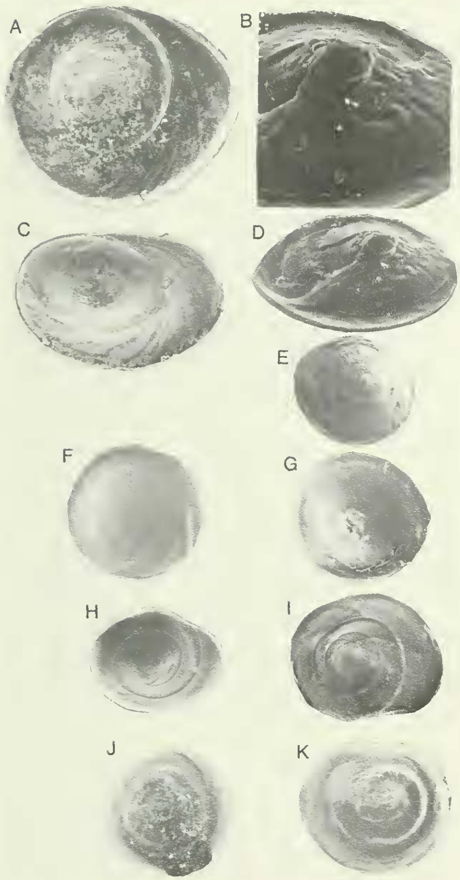

FIG. 9. Operculae of *Phreatodrobia nugax nugax* (A–E), *P. micra* (F, G; Locality 3), *P. rotunda* (H, I; Locality 3), and *P. imitata* (J, K; Locality 20). Operculum lengths are as follows: A (0.63 mm), C (0.57 mm)(Locality 3); B (ventral aspect, left-right distance, 0.29 mm), D (ventral aspect, 0.56 mm)(Locality 4); E (ventral aspect, 0.536 mm; Locality 24); F (0.29 mm), G (ventral aspect, 0.29 mm), H (0.536 mm), I (ventral aspect, 0.609 mm), J (0.29 mm), K (ventral aspect,, 0.314 mm).

second pair of basal cusps on the central radular tooth, seen in some populations of this species, are unique in the genus. Two subspecies are recognized on the basis of differences in shell morphology. Karnei (1978) described shells of this species (as Gastropod Genus No. 1) from Brackenridge Zoo Well. Longley (1975, 1981) incorrectly identified specimens of this species from the SWTSU Well as *P. micra*.

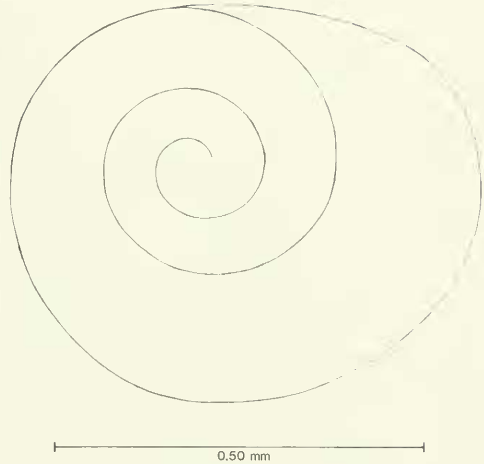

FIG. 10. Operculum of *Phreatodrobia nugax nugax* (Locality 3).

DESCRIPTION. The shell has 2.5–3.2 whorls and averages 0.93–1.71 mm in width. The protoconch, sometimes tilted (Fig. 3I), has 1.25–1.50 moderately pitted whorls (Fig. 7A, B). Axial growth lines are typically well developed on the teleoconch (Fig. 4), which may also have collabral costae (Fig. 4U). General shell form is highly variable in some populations. For the San Marcos Springs population, most individuals have the typical low trochoid shell (Fig. 4C), yet occasional

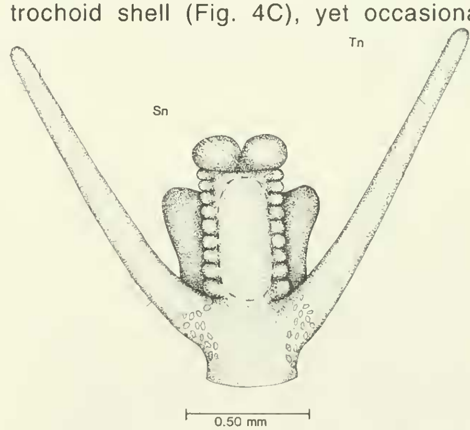

FIG. 11. Dorsal aspect of head of *Phreatodrobia nugax*. Note the presence of granules in the base of the tentacles (Tn), and the ciliation on the tentacle tips and along the outside edge of the base of the left tentacle. The dashed lines on the snout (Sn) indicate the position of the buccal mass. The anterior end of the foot is shown beneath the snout. Sn = snout; Tn = tentacle.

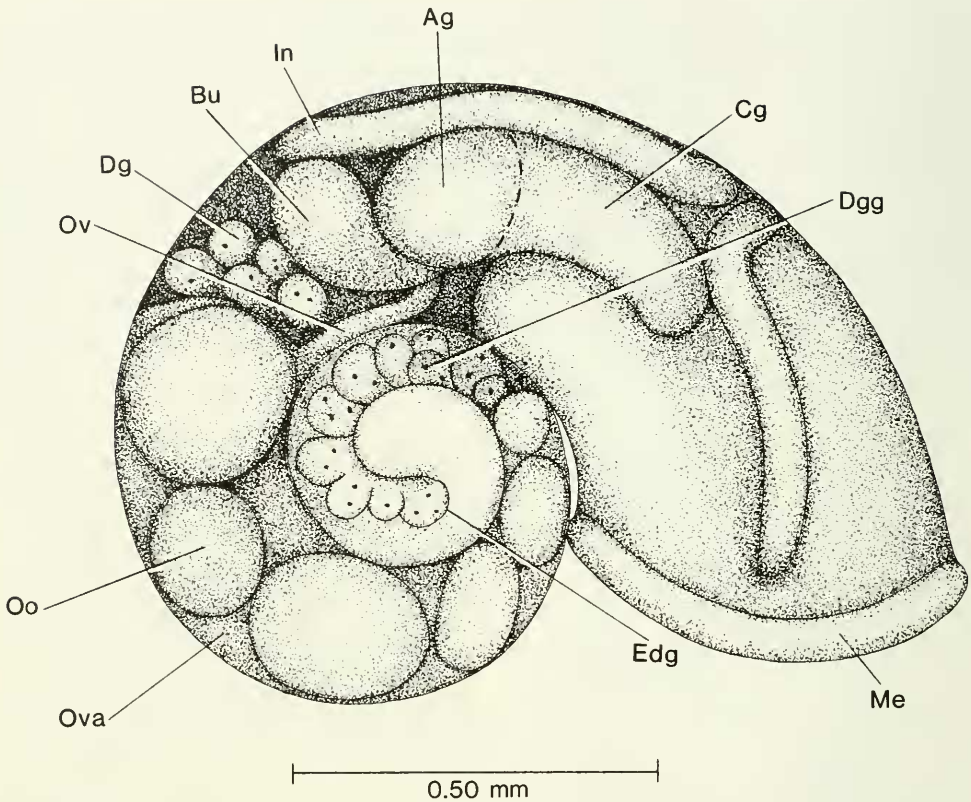

FIG. 12. Morphology of a female *Phreatodrobia nugax* (minus the head-foot), as seen from the right (and slightly dorsal) side. The kidney tissue is not shown. Ag = albumen gland; Bu = bursa copulatrix; Cg = capsule gland; Dg = digestive gland; Dgg = digestive gland granule; Edg = posterior end of digestive gland; In = intestine; Me = mantle edge; Oo = oocyte; Ov = oviduct; Ova = ovary.

smaller individuals with near-planispiral shells (Fig. 4H) were also found. Shell form in the Barton Springs population varies from near-planispiral to low trochoid, to low trochoid with costae, to low conical (Fig. 4M, Q, U, Y, Z). The aperture is moderately flared all around, with flaring most pronounced in large individuals. While typically wider than long and near-circular, aperture shape can be modified (especially in large-sized individuals from San Marcos Springs and the SWTSU Well) by a slight adapical notch or a pronounced abaxial fluting of the outer lip. The aperture is free from the body whorl in 0–70% of the samples from given populations, with populations with large-sized individuals having the highest incidence. The inner lip is especially thickened. The white thickening of the end of the body whorl was seen in all fresh specimens.

The operculum has 2.5 whorls (Fig. 10), with the nucleus positioned at about 43% of the operculum length, and varies from near-circular to ellipsoidal in shape (Fig. 9A, C, E). Only individuals from San Marcos Springs and the SWTSU Well typically have a well-developed thickening on the ventral opercular surface. In these populations the operculum has a low conical shape, with the process consisting of extra layers of material deposited at the apex (operculum nucleus) of the cone (which points into the foot). The process is less prominent and elevated than that of *P. micra* (compare Fig. 9B, D with Fig. 9G). In other populations the operculum is flatter

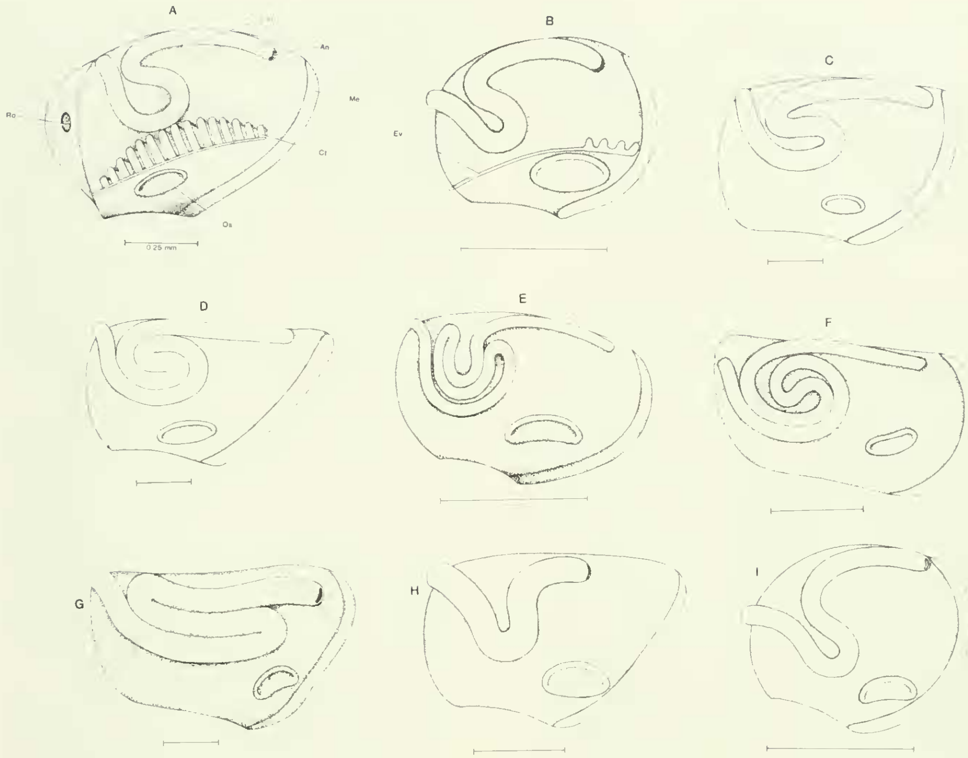

FIG. 13. Contents of the pallial cavity of *Phreatodrobia nugax* (A), *P. micra* (B), *P. conica* (C), *P. imitata* (D), *P. plana* (E), *P. punctata* (F), *P. rotunda* (G), *Balconorbis uvaldensis* (H), and *Stygopyrgus bartonensus* (I). The pallial roof has been slit along its length on the extreme right side and then folded over to the left and pinned. The pallial reproductive organs are not shown and the kidney is figured only in A. All scale bars equal 0.25 mm. An = anus; Ct = ctenidium; Ev = efferent branchial vessel; In = intestine; Me = mantle edge; Os = osphradium; Ro = renal opening.

and the process reduced or virtually absent (Fig. 9E).

Anatomical description is based on extensive study of material from San Marcos Springs and lesser study of populations from Barton Springs and wells owned by SWTSU (including live material), Longhorn Portland Cement Company, Union Stockyards, Brackenridge Zoo, and W. C. Reagan.

The snout (Fig. 11) is longer than wide, with folds along its sides. The pink-colored (haemoglobin) buccal mass is readily seen through the snout. The tentacles are elongate, rounded at the tips, moderately thickened relative to snout width, and held at 60–100 degrees to one another. Stiffened, elongate cilia fringe the tentacle tips. Four to five hypertrophied ciliary tufts line the outer side of the left tentacle near its base. White granules are clustered at the base of the tentacles and clear crystalline granules extend back along the "neck." The foot is long and slender, broad anteriorly and tapered posteriorly. The pedal glands consist of a single massive central gland flanked by seven to eight smaller glands on either side. Crystalline granules are found on the sides of the foot. The shell is carried with the coiling axis tilted about 30 degrees to the plane of the substrate. The intestine, gonad (ovary, white; testis, yellow), and pallial gonoduct (oviduct, white; prostate, green) are visible through the shell.

The ctenidium typically occupies 75% of the

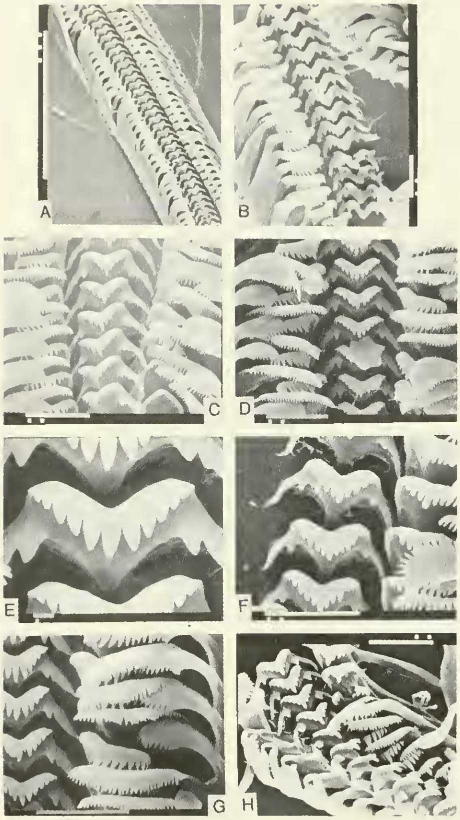

FIG. 14. Radulae of *P. nugax nugax* (A, C–H) and *P. nugax inclinata* (B). The localities are as follows: A, F (Locality 2), B (Locality 11), C (Locality 3), D, E, G (Locality 4), H (Locality 14). The scale bars equal 0.1 mm (A), 0.01 mm (B–D, F–H), or 0.001 mm (E).

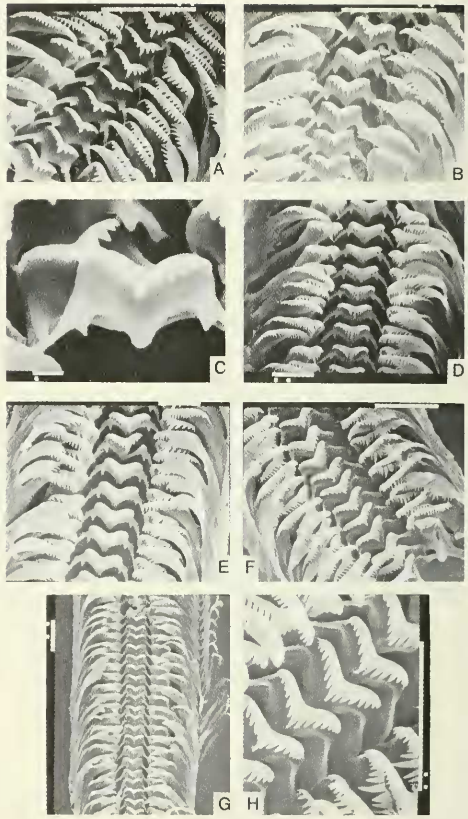

FIG. 15. Radulae of *Phreatodrobia micra* (A–C; Locality 3), *P. rotunda* (D, E; Locality 3) and *P. imitata* (F–H; Locality 20). Scale bars equal 0.01 mm (A, B, D–H) or 0.001 mm (C).

pallial cavity length (Fig. 13A). The ctenidial filaments are triangular in shape (when dissected out and laid flat), almost twice as long as wide, well-ciliated, and moderately thickened. The broadest part of the filament is positioned at almost two-thirds of the filament length. The osphradium occupies 22–28% of the pallial cavity length in all populations except that from the Union Stockyards Well (41%), which consists of very small-sized individuals. The osphradium is centered towards the posterior end of the ctenidium, with 20–30% of the ctenidium posterior to the end of the osphradium.

The central radular tooth is trapezoidal in shape with well developed lateral angles. A second pair of basal cusps on the central tooth was seen only in individuals from San Marcos Springs and the SWTSU Well. The inner marginal tooth is noteworthy for the large number of cusps it possesses (24–34) relative to other congeners. The stomach has a small caecal appendix (Fig. 18A). Note that the anterior arm of the U-shaped intestine loop in the pallial roof bends back posteriorly before turning anteriorly (Fig. 13A) (compare to simpler U-shaped loop in *P. micra*, Fig. 13B). The loop usually abuts against the longest gill filaments.

The testis (Fig. 19D) consists of simple lobes joining a central basal mass. The vas deferens exits at a point 25–30% back along the testis length. The seminal vesicle (Sv)

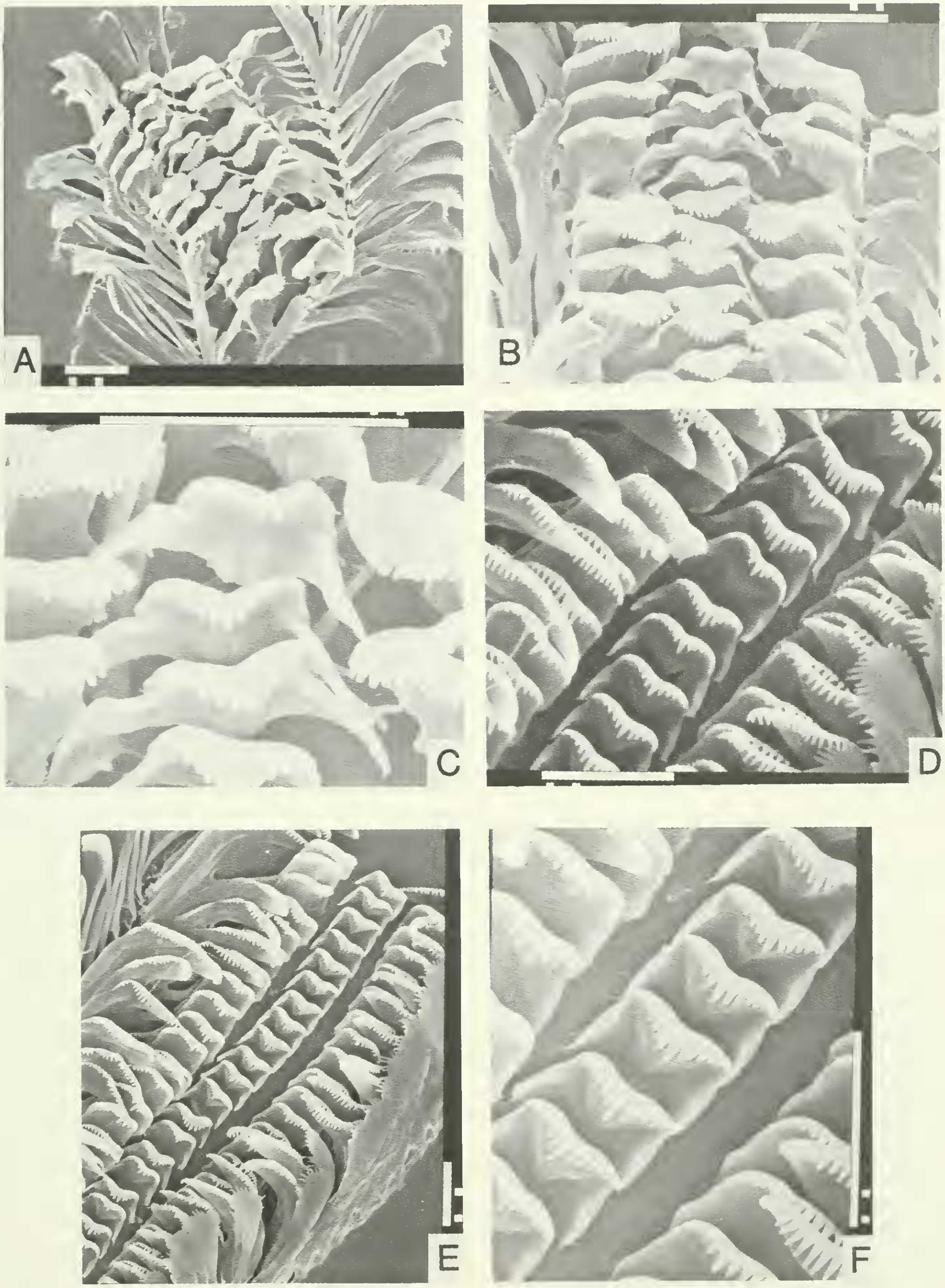

FIG. 16. Radulae of *Phreatodrobia plana* (A–C; Locality 3) and *P. conica* (D–F; Locality 5B). All scale bars equal 0.01 mm.

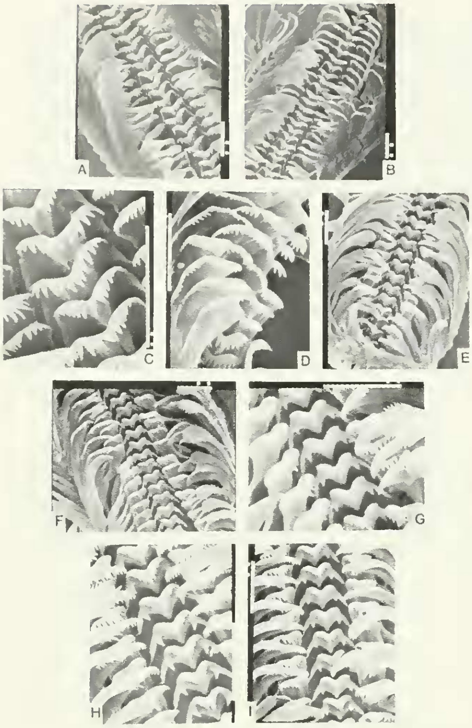

FIG. 17. Radulae of *Phreatodrobia punctata* (A–D), *Balconorbis uvaldensis* (E–G), and *Stygopyrgus bartonensus* (H, I). All scale bars equal 0.01 mm.

consists of a few, non-thickened coils largely hidden under the anterior portion of the testis. The anteriormost 52% of the prostate is pallial.

The penis (Fig. 19A, B) is about three times as long as the snout and has pronounced lobes along much of the inner curvature. The short penial filament lacks folds and has columnar epithelium (Co) along its sides. Long cilia are active along much of the length of the penial filament and extend onto the folds of the inner curvature. The penial folds have a glandular edge (not figured), and occasional glandular clusters (spherical bodies, Fig. 19A) are present along the penial length. The vas deferens undulates slightly in the penis.

The large ovary (Ova) lacks pronounced lobation and typically contains six to ten oocytes (Oo) of various sizes (Fig. 12). The anterior end of the ovary abuts against the stomach. The oviduct exits near the anterior end of the ovary and disappears beneath the bursa. The capsule gland is twice as long as the albumen gland. The ventral channel is narrow and has a pronounced lateral fold (not figured). The anterior end of the capsule gland terminates in a muscularized S-shaped coil (Fig. 20A) or simple twist (Fig. 20B) to the left side (populations from San Marcos and Barton Springs, SWTSU Well, Longhorn Portland Cement Company Well), or lacks such modifications and has a subterminal capsule gland opening (population from Union Stockyards Well). The development of the coil correlates with body size: larger females from Barton Springs, for instance, have the S-shaped coil while smaller individuals have a simple twist. The oviduct coil lies partly posterior to the albumen gland (Fig. 20A). The seminal receptacle opens into the end of the oviduct coil (right side) just posterior to the point where the short bursal duct joins the oviduct (Fig. 20C). The seminal receptacle always has a pink sheen as does the rather swollen oviduct coil, suggesting that the latter may also serve to store sperm. The bursa is flimsy in texture and was easily ruptured during dissection.

HOLOTYPE. ANSP 77574 (Fig. 4A, F, J).

TYPE-LOCALITY. Drift debris of Guadalupe River about four miles above New Braunfels, Comal County (Fig. 1, Locality 6).

DISTRIBUTION. Edwards (Balcones Fault Zone) Aquifer, and (possibly) Cow Creek and Glen Rose Aquifers in Travis, Hays, Comal, Kendall, Bexar, and Uvalde Counties (Fig. 1, Localities 1–4, 6, 8–12, 14, 26).

VARIATION. The large shell form variation seen in the populations from San Marcos and Barton Springs requires comment. Living specimens of the smaller, flat "form" from San Marcos Springs were always found encrusted with epigean epibionts whereas the more typical trochoid "form" was always found clean. A different habitat is suggested for these two "forms", with the former perhaps dwelling at or very near to the groundwater outlet. We do not know whether this dimorphism is phenotypic or genetic. The shells of living specimens of all Barton Springs "forms" were always clean. We suspect that this population is highly variable because it is of hybrid origin, with incompletely formed species having been brought into sympatry. More work is needed to sort out the systematics of this polytypic species.

DISCUSSION. *Phreatodrobia nugax* was originally described as a subspecies of *P.*

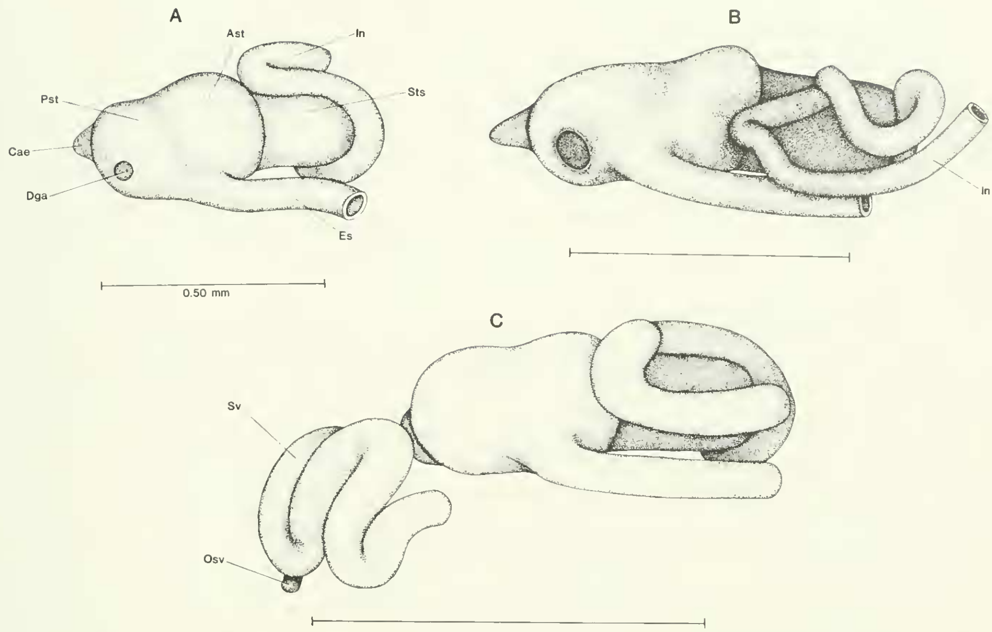

FIG. 18. Stomachs of *Phreatodrobia nugax* (A), *P. rotunda* (B), and *P. punctata* (C). Note the lack of external differentiation of the stomach chambers (Ast, Pst), and the coiling of the intestine (In) on the style sac (Sts) in B and C. The thickened coils of the seminal vesicle (Sv) of *P. punctata* are also figured in C. Ast = anterior stomach chamber; Cae = caecal appendix; Dga = digestive gland opening; Es = oesophagus; In = intestine; Osv = opening of seminal vesicle into testis; Pst = posterior stomach chamber; Sts = style sac; Sv = seminal vesicle.

micra and there has been some question as to whether these taxa are separate species (Fullington, 1978). We collected both species at three localities, two of which were caves from which only empty shells were obtained, the third of which was San Marcos Springs, from which living specimens of both species were obtained. As indicated above, there is more than sufficient anatomical evidence to merit separate species status for the San Marcos Springs populations. Note that at this locality the two species differ very significantly ($p < .001$, Mann-Whitney U Test) in size (shell width, data from Appendix 2). At the other two localities, Honey Creek Cave and Century Caverns, the size difference is somewhat less significant ($p < .05$). The shell shape difference between species is pronounced in samples from all three of these localities as well as for the type-specimens (which were also collected together at the same locality): compare Figs. 3F, J, N with 4A, F, J; 3R, S, T with 4O; 3M, Q with 4S, W; and 3H, L, P with 4C, H, L. A shell height versus shell width plot for samples from given populations readily separates the two species (Fig. 22). Such pronounced differences in shell size and shape in sympatric populations suggests that two species exist at these localities (as well as in San Marcos Springs). It should be noted, however, that *P. nugax* can apparently converge on *P. micra* when found alone. Individuals from Union Stockyards Well have the very low spire, small size, and relatively large osphradium typical of *P. micra* (but have a complete ctenidium).

Phreatodrobia nugax nugax

MATERIAL EXAMINED. As for the species, excluding Longhorn Portland Cement Company Well.

DIAGNOSIS. Shell variable in size and form. Protoconch without tilt. Aperture rounded, free from or touching the penultimate whorl;

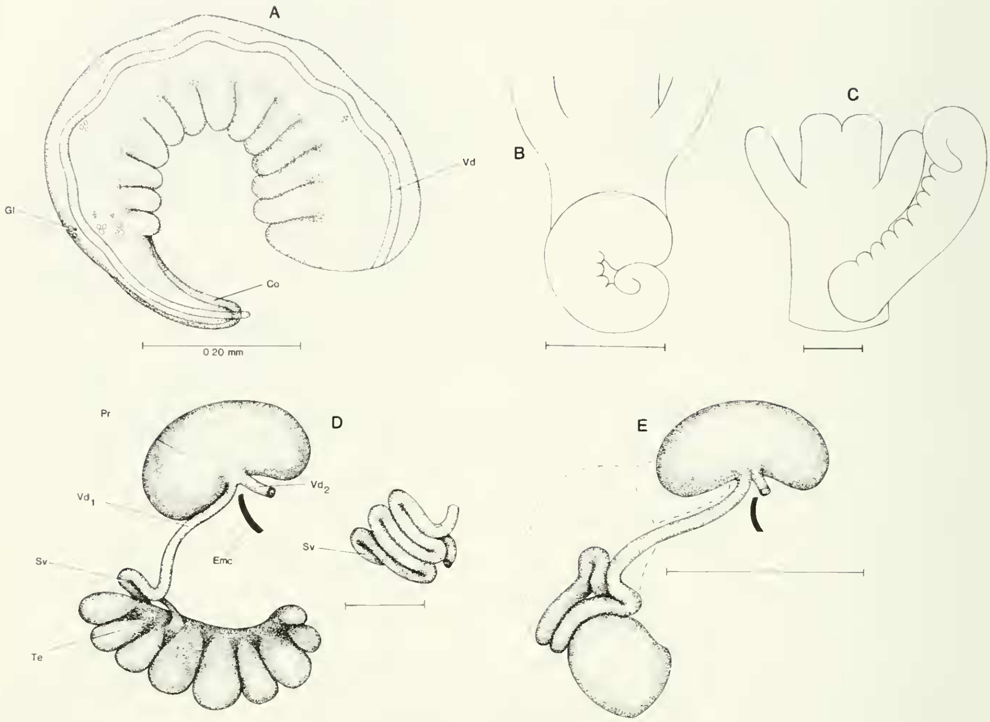

FIG. 19. Male reproductive morphology. A, B. Penis (dorsal aspect) of *Phreatodrobia nugax*. C. Penis (dorsal aspect) of *P. rotunda*. Note that the penis does not coil on the "neck" as in B. D. Testis (Te), Seminal vesicle (Sv), and prostate (Pr) of *P. nugax*. Note that about half of the prostate length is pallial. E. Testis (posterior portion not shown), seminal vesicle, and prostate of *P. plana*. The dashed lines indicate the position of the stomach. Co = columnar epithelium; Emc = posterior end of pallial cavity; Gl = glandular units; Pr = prostate; Sv = seminal vesicle; Te = testis; Vd = vas deferens; Vd_1 = vas deferens from seminal vesicle to prostate; Vd_2 = vas deferens from prostate to penis.

inner lip thickened and slightly to moderately flared. Apertural plane with or without slight tilt relative to coiling axis.

Phreatodrobia nugax inclinata Hershler & Longley, new subspecies

MATERIAL EXAMINED. BEXAR COUNTY: Longhorn Portland Cement Company Well.

DIAGNOSIS. Shell (Figs. 3A–E, I) only slightly wider than tall, of globose appearance, with protoconch tilted at 20°–30° relative to the teleoconch (Fig. 3I). Aperture fused to (not merely touching) the penultimate whorl; inner lip thin and flared only at fusion point. Aperture slightly angled anteriorly, apertural plane highly tilted (>30°) relative to shell axis.

REMARKS. The protoconch tilting and apertural peculiarities distinguish this subspecies from *P. n. nugax*. No anatomical differences were seen.

HOLOTYPE. ANSP 359089 (Fig. 3A, B).

PARATYPES. ANSP A10623D.

TYPE-LOCALITY. Longhorn Portland Cement Company Well (Fig. 1, Locality 11).

DISTRIBUTION. Thus far known only from the type-locality.

ETYMOLOGY. The subspecific epithet refers to the inclined or tilted position of the protoconch in this subspecies.

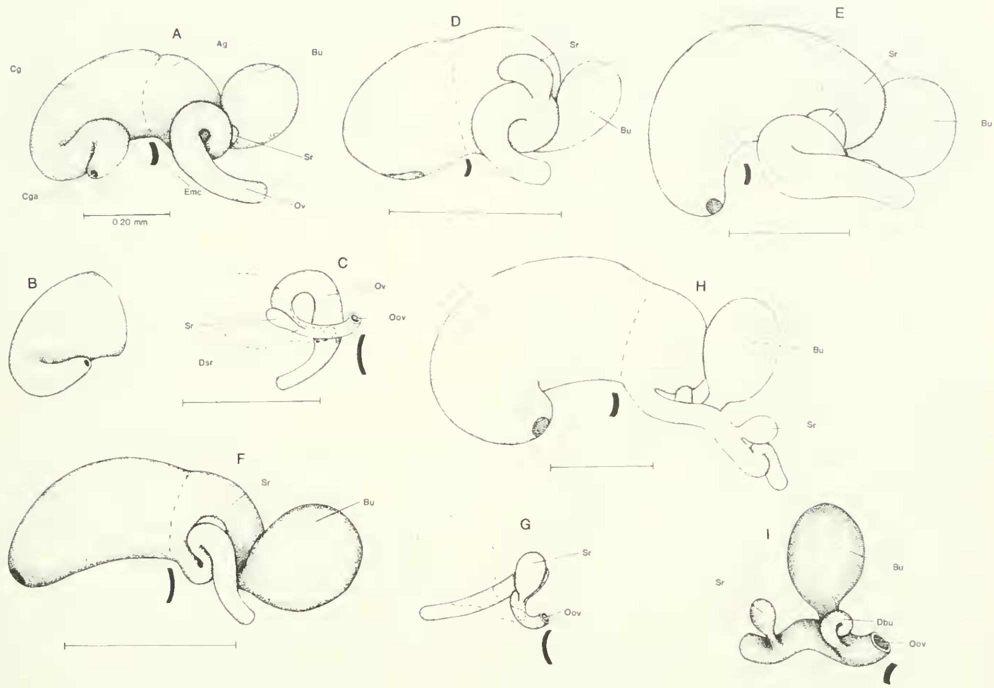

FIG. 20. Female reproductive morphology of *Phreatodrobia nugax* (A–C), *P. micra* (D), *P. conica* (E), *P. plana* (F, G), and *P. rotunda* (H, I). The left aspect is shown in A, B, D, E, F, and H; the right aspect is shown in all other figures. Only the anterior end of the capsule gland (Cg) is shown in B. Note the variation in coiling of the anterior end of the capsule gland (Cg) in *P. nugax* (A, B). All scale bars equal 0.2 mm. A and B have the same scale. Ag = albumen gland; Bu = bursa copulatrix; Cg = capsule gland; Cga = capsule gland opening; Dbu = duct of bursa copulatrix; Dsr = duct of seminal receptacle; Emc = posterior end of pallial cavity; Oov = opening of oviduct into pallial oviduct; Ov = oviduct; Sr = seminal receptacle.

Phreatodrobia rotunda Hershler & Longley, new species
Fig. 5E, F, I, J, 7E, 9H, I, 13G, 15D, E, 18B, 19C, 20H, I

MATERIAL EXAMINED. HAYS COUNTY: SWTSU Well; San Marcos Springs.

DIAGNOSIS. A large-sized species (shell width 2 mm). Shell (Fig. 5E, F, I, J) planispiral, with flattened base. Operculum (Fig. 9H, I) multi-whorled and striated. Ctenidium absent (Fig. 13G); osphradium short relative to pallial cavity length (13%). Central tooth of radula with a single pair of basal cusps (Fig. 15D, E). Style sac length 70% of that of stomach (Fig. 18B); intestine with complex coil on style sac (In, Fig. 18B) and narrow, elongate U-shaped loop in pallial roof; long axis of loop parallel to length of pallial cavity (Fig. 13G). Ovary and testis fill small portion (22%, 21%) of digestive gland length. Penis enlarged and without tight coil (Fig. 19C). Bursa duct coiled (Dbu, Fig. 20I); oviduct opens into anterior end of albumen gland.

REMARKS. This species is distinguished from other congeners by the following unique character-states: large planispiral shell, striated operculum, complex intestine coil on style sac, and very small-sized ovary and testis.

DESCRIPTION. Morphological description is based on study of material from San Marcos Springs. The shell has 3.0–3.8 whorls and varies from 1.83–2.16 mm in width. The protoconch, hidden (in apertural view) by rapidly expanding teleoconch whorls, has 1.25

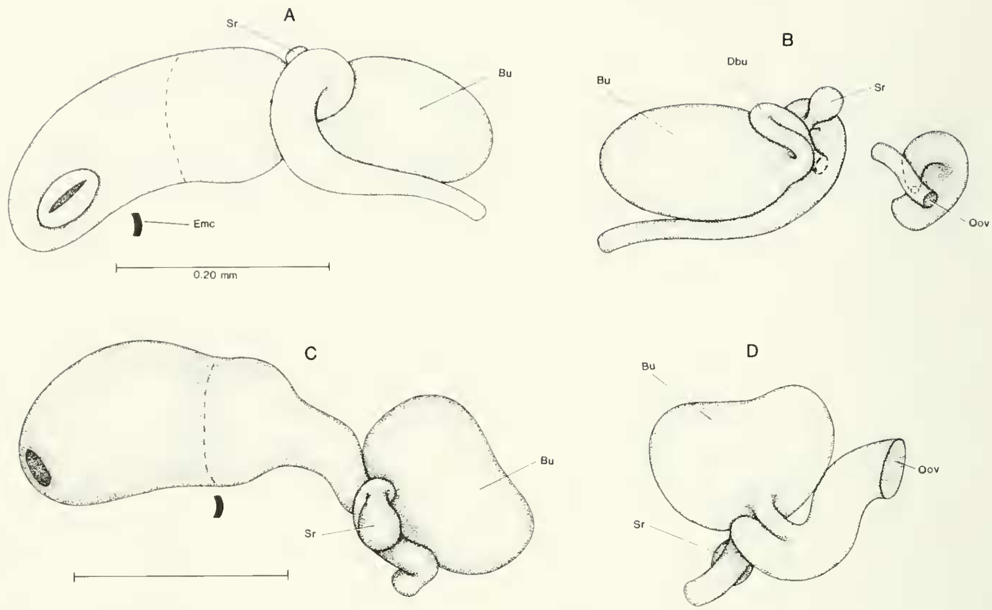

FIG. 21. Female reproductive morphology of *Phreatodrobia imitata* (A, B) and *P. punctata* (C, D). The left aspect is shown in A and C, and the right aspect in B and D. Note the muscularized capsule gland opening of *P. imitata* (A). All scale bars equal 0.2 mm. Bu = bursa copulatrix; Dbu = duct of bursa copulatrix; Emc = posterior end of pallial cavity; Oov = opening of oviduct into pallial oviduct; Sr = seminal receptacle.

whorls, the first whorl of which is marked by small pits, followed by a quarter whorl having strong, elevated growth lines (Fig. 7E). The teleoconch has fine growth lines. The apertural lip is relatively thin and appears broadly notched adapically when seen from above (Fig. 5I). The aperture is rounded and flared above and below. The inner lip is fused to the penultimate whorl. The outer lip is advanced relative to the remaining peristome, often angled or twisted (Fig. 5E), and is not flared. Note that the aperture does not extend above the penultimate whorl (Fig. 5E, F).

The operculum (Fig. 9H, I) is extremely thin, arched into a low cone, and has about five whorls. The ventral surface is smooth. The nucleus is positioned at about 44% of the operculum length. As for other *Phreatodrobia* that have a thin operculum, the operculum has a very light amber tint. Note the unusual operculum shape, with a sudden narrowing to the right in Fig. 9H. A large number of short, deep striations are arranged in rows which cross the growth lines at a high angle.

The central tooth of the radula is quite broad, as the lateral angles diverge at a high angle. The caecal appendix is enlarged compared to that of *P. nugax* (Fig. 18A, B). The intestine coil on the style sac sometimes extends onto the stomach. The U-shaped intestine loop in the pallial cavity roof is twice as long as wide and extends far into the anterior half of the pallial cavity (Fig. 13G).

The ovary and testis consist of a single solid mass. The vas deferens exits from the anterior end of the testis and has a few coils posterior to the stomach. The anteriormost 60% of the prostate is pallial. The penis is about four times as long as the snout and does not coil on the neck, but extends anteriorly (Fig. 19C). The capsule gland is more than twice as long as the albumen gland (Fig. 20H) and has a slight twist at its anterior end with a terminal opening. The section of oviduct anterior to the seminal receptacle is often swollen and has a pink sheen. The coiled bursa duct is shown in Fig. 20I. The seminal receptacle is positioned posterior to the bursa

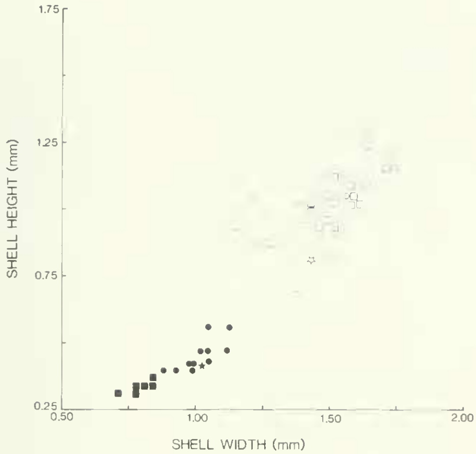

FIG. 22. Plot of shell height versus shell width for sympatric populations of *Phreatodrobia nugax* and *P. micra*. The populations represented are from San Marcos Springs (open square, *P. nugax*; filled square, *P. micra*) and Century Caverns (open circle, *P. nugax*; filled circle, *P. micra*). Type specimens for the two species are indicated by an open (*P. nugax*) or filled (*P. micra*) star. Note the clear separation between the species in the plot.

and albumen gland, and opens via a short duct anterior to the oviduct coil, and well posterior to the point where the bursa duct joins the oviduct (Fig. 20H, I).

HOLOTYPE. ANSP 359090 (Fig. 5E).

PARATYPES. ANSP A10623E.

TYPE-LOCALITY. San Marcos Springs (Fig. 1, Locality 3).

DISTRIBUTION. Edwards (Balcones Fault Zone) Aquifer in Hays County (Fig. 1, Localities 3, 4).

ETYMOLOGY. The epithet refers to the rounded outline of the shell of this species.

Phreatodrobia conica Hershler & Longley, new species
Figs. 5M–P, 7C, 8C, 13C, 16D–F, 20E

MATERIAL EXAMINED. COMAL COUNTY: Hueco (A, B) Springs; Honey Creek Cave. BEXAR COUNTY: City Water Board Artesian Station, Well 4.

DIAGNOSIS. Shell (Fig. 5M–P) large for genus (shell height 1.7 mm), conical, with a simple aperture and usually with a varix near the end of the body whorl (Fig. 5P). Teleoconch surface mottled with numerous short ridges. Ctenidium absent, osphradium filling 20% of the pallial cavity length (Fig. 13C). Central tooth of radula square-shaped and without basal cusps (Fig. 16D–F). Style sac length 79% of that of stomach; intestine loop in pallial roof U-shaped and with long axis parallel to pallial cavity length (Fig. 13C). Ovary and testis fill 30–40% of digestive gland length. Pallial portion of prostate relatively small; penis greatly elongate relative to snout. Oviduct enters anterior end of albumen gland.

REMARKS. Distinguishing features for this species include the conical shell with unusual sculpture pattern of small ridges, square-shaped central radular tooth, and small proportion of pallial prostate.

DESCRIPTION. The shell has 3.5–4.0 rounded whorls, a pronounced spire, and varies from 1.49–1.86 mm in height. The pits on the 1.5 protoconch whorls are well developed (Fig. 7C). Teleoconch sculpture consists of a large series of short ridges that are aligned at a slight angle to the whorl length. The ridges are occasionally elevated, particularly near the end of the body whorl, producing a mottled effect (Figs. 5O, 7C, 8C). Thickened axial growth lines are also present on the last half of the body whorl. Note that the ridges often converge and may be largely or totally absent in worn sections of the teleoconch (Fig. 5N). Seventy-three percent of adult shells from Hueco Springs (A, B) have a varix behind the aperture. The aperture is non-circular, thickened all around, and usually slightly separated from the penultimate whorl in adult shells.

Description of operculum and anatomy is based on study of specimens from Hueco (B) Springs. The operculum is flat, with about three whorls, and is slightly longer than wide. The nucleus is positioned at about 41% of the operculum length. Spiral growth lines are well developed on its surface.

The lateral angles of the central radular teeth project downwards instead of outwards, resulting in the unusual square shape of the tooth (Fig. 16D–F). Note that the lateral teeth sometimes have 10 or more cusps on one side of the central tooth (Fig. 16E). The stomach has a small caecal appendix.

The testis, unlobed as is the ovary, fills 42% of the digestive gland length. The seminal vesicle exits from the anterior end of the testis and coils posterior to the stomach. Only the anteriormost 33% of the prostate is pallial. The penis is seven-eight times as long as the snout (preserved specimens) and has a somewhat thickened filament (not figured). The capsule gland is more than twice as long as the albumen gland and its anterior end bends back towards the end of the pallial cavity (Fig. 20E). The capsule gland opening is terminal. The tight oviduct coil is appressed against the posterior portion of the pallial oviduct, with the seminal receptacle opening into the right (inner) side of the coil. The short bursa duct joins the oviduct just before the opening into the albumen gland (not figured).

HOLOTYPE. ANSP 359086 (Fig. 5M).

PARATYPES. ANSP 359087/A10623B.

TYPE-LOCALITY. Hueco (B) Springs, Comal County (Fig. 1, Locality 6).

DISTRIBUTION. Edwards (Balcones Fault Zone) and possibly Cow Creek Aquifers in Comal and Bexar Counties (Fig. 1, Localities 6, 9, 13).

ETYMOLOGY. The epithet refers to the conical shell shape of this species.

Phreatodrobia plana Hershler & Longley, new species
Figs. 5A–D, G, H, K, L, 7F, 13E, 16A–C, 19E, 20F, G

MATERIAL EXAMINED. HAYS COUNTY: SWTSU Well, San Marcos Springs. COMAL COUNTY: Comal Springs; Natural Bridge Caverns.

DIAGNOSIS. A small-sized species with shell width ranging from 0.75–1.1 mm. Shell (Fig. 5A–D, G, H, K, L) planispiral, base flattened, aperture extends above penultimate whorl (Fig. 5A–C). Teleoconch sculpture consists of thickened, wrinkled collabral lines (Fig. 7F). Ctenidium absent, osphradium filling 33% of pallial cavity length (Fig. 13E). Central tooth of radula without basal cusps; lateral tooth lacking enlarged central cusp (Fig. 16A–C). Stomach length more than twice that of style sac (Fig. 19E); intestine coil in pallial roof complex (Fig. 13E). Ovary and testis fill 50–60% of digestive gland length. Oviduct enters anterior end of albumen gland (Fig. 20F).

REMARKS. Distinguishing features include the minute planispiral shell with adapically extended aperture, teleoconch sculpture consisting of thickened, wrinkled collabral lines, and the complex intestine coil in the pallial roof.

DESCRIPTION. The shell has 2.75–3.0 whorls and, while extremely small in the Comal and San Marcos Springs populations (shell width, <0.88 mm), often exceeds 1.00 mm in width in specimens from Natural Bridge Caverns. Note that the shells from Natural Bridge Caverns are considerably more flattened than those from San Marcos Springs. The whorls are rounded at the periphery and somewhat angled above and below. The protoconch is largely overlapped by the first teleoconch whorl (Fig. 7F). The first half whorl of the protoconch is covered with shallow pits which are joined by the thickened, wrinkled lines on the final protoconch whorl. Note how these thickened lines often converge on the teleoconch and appear plicate in places (Fig. 7F, upper left corner). These collabral lines are not well pronounced on the worn shells collected from Natural Bridge Caverns (Fig. 5D, H, L). The aperture is longer than wide, fused to the body whorl (Fig. 5B, C, D), and thickened all around. While extending above the penultimate whorl, the aperture does not extend below the flattened base. The lip is often fluted back ad- and abapically (appearing notched when seen from above and below), and the outer lip is bent adaxially in specimens from Natural Bridge Caverns (Fig. 5D) and Comal Springs (not figured).

Description of the operculum and anatomy is based on study of specimens from the SWTSU Well. The flat operculum is somewhat longer than wide, with about three whorls. The nucleus is positioned at about 40% of the operculum length. The lateral angles of the central radular tooth diverge at a high angle, producing an elongate trapezoidal shape for the tooth (Fig. 16B, C). Note the large number of cusps on the lateral tooth (often exceeding 20 for the entire row) and lack of enlarged central cusp. The stomach lacks a caecal appendix. The simple U-shaped intestine loop in the pallial roof, typical of *Phreatodrobia*, is modified in this species by addition of an extra, final loop outside of the preceding loop (Fig. 13E). Note that the long axes of the loops are oriented perpendicular to the pallial cavity length.

The testis and ovary are unlobed and fill 59% and 52% of the digestive gland length. The seminal vesicle exits from the anterior end of the testis and coils on the posterior part of the stomach (Fig. 19E). The anteriormost 47% of the prostate is pallial. The penis is about three times as long as the snout. The capsule gland is about twice as long as the albumen gland and has a terminal opening

(Fig. 20F). The oviduct coil is appressed to the left side of the albumen gland: note that the coil is counter-clockwise, not clockwise as is typical for the genus (Figs. 20A, D, E, 21A). The seminal receptacle opens into the right side of the oviduct coil just posterior to where the bursa duct enters (Fig. 20G).

HOLOTYPE. ANSP 359091 (Fig. 5A).

PARATYPES. ANSP A10623F.

TYPE-LOCALITY. San Marcos Springs, Hays County (Fig. 1, Locality 3).

DISTRIBUTION. Edwards (Balcones Fault Zone) and possibly Glen Rose Aquifers in Hays and Comal Counties (Fig. 1, Localities 3, 4, 8).

ETYMOLOGY. The epithet refers to the planispiral shell of this species.

Phreatodrobia imitata Hershler & Longley, new species
Figs. 6A–G, 8A, B, D, 9J, K, 13D, 15F–H, 21A, B

MATERIAL EXAMINED. BEXAR COUNTY: Verstraeten Well; O. R. Mitchell Well.

DIAGNOSIS. Shell (Fig. 6A–G, 8A, B, D) elongate-conical, height about 1 mm, with highly flared aperture. Teleoconch sculpture consisting of collabral costae and spiral lines. Ctenidium absent (Fig. 13D); osphradium filling 26% of pallial cavity length. Central tooth of radula without basal cusps (Fig. 15F–H). Style sac length two-thirds that of stomach; intestine coil in pallial cavity complex (Fig. 13D). Ovary and testis filling 30–40% of digestive gland length. Bursa duct coiled (Fig. 21B); oviduct entering posterior end of albumen gland; capsule gland opening with muscularized lip (Fig. 21A).

REMARKS. Distinguishing features of this species include the shell sculpture, consisting of collabral costae and spiral lines, complex intestine coil in pallial roof, and muscularized lip surrounding the capsule gland opening. Partial descriptions for this species were provided by Fullington (1978; for *Paludiscala* sp.) and Karnei (1978; for Gastropod Genus No. 2, Species 1 and 2) (both unpublished theses).

DESCRIPTION. The shell has 3.3–3.5 well-rounded whorls with deep sutures. Shell height averaged 1.01 mm for the Verstraeten Well sample and 1.03 mm for the O. R. Mitchell Well sample. The pits on the 1.0–1.25 protoconch whorls are well-developed (Fig. 6F). Spiral lines begin at the end of the protoconch and appear slightly wrinkled under high magnification (Fig. 8D). The lines cross the collabral costae (Figs. 6D, 8B). Low collabral ridges run between the costae and join the spiral lines (Fig. 8B, D). Costae are sometimes absent on the first 0.5–1.0 protoconch whorl (Fig. 6E). The costae are typically low (as in Figs. 6B, C, D, 8A, B): broad, lamelliform costae were not seen in the sample from O. R. Mitchell Well (n = 14) and were seen in only 10% of a sample from the Verstraeten Well (n = 32). Note that the lamelliform costae are not oriented perpendicular to the whorl surface, but curve (to the left in Fig. 6D). The aperture is rounded, moderately thickened, and highly flared, although flaring of the adapical lip is sometimes reduced (Fig. 6E). The aperture is sometimes loosened from the penultimate whorl. The umbilicus is open (Fig. 6G).

Anatomical description is based on study of material from Verstraeten Well. The thin operculum (Fig. 9J, K) is about as long as it is wide, with the nucleus positioned at about 40% of the operculum length. The ventral opercular surface is near smooth, with only a very small, low process (Fig. 9K).

The central tooth of the radula is trapezoidal in shape (Fig. 15F–H) and has especially narrow and elongate cusps. The stomach lacks a caecal appendix. The coil of the intestine in the pallial cavity roof (Fig. 13D) is modified by addition of an extra loop to the inside of the preceeding one. Note that the long axes of the loops are oriented parallel to the pallial cavity length.

The ovary and testis consist of a single solid mass and fill 34% and 28% of the digestive gland length. The vas deferens exits from the anterior end of the testis and coils posterior to the stomach. The anteriormost 45% of the prostate is pallial. The penis is only twice as long as the snout. The capsule gland is about one and a half times the length of the albumen gland (Fig. 21A). Note that a larger proportion of the capsule gland is pallial than typical for the genus. The narrow capsule gland opening is sub-terminal and surrounded by a muscular lip which measures 0.08 mm × 0.06 mm. The oviduct coil is partly posterior to the albumen gland. The short duct of the bursa loops back onto the right side of the bursa and joins the oviduct just before the opening into the posterior end of the albumen gland (Fig. 21B). Note that the bursa is oriented with its long axis parallel to the length of the pallial oviduct.

HOLOTYPE. ANSP 359088 (Fig. 6A).

PARATYPES. ANSP A10623C.

TYPE-LOCALITY. Verstraeten Well, Bexar County (Fig. 1, Locality 20).

DISTRIBUTION. Edwards Balcones Fault Zone) Aquifer in the Von Ormy Section of Bexar County (Fig. 1, Localities 20, 21).

ETYMOLOGY. The epithet refers to the convergence in shell form between this species and *Paludiscala* Taylor, 1966.

Phreatodrobia punctata Hershler & Longley, new species

Figs. 6H, I, 7C, 8E, 13F, 17A–D, 18C, 21C, D

MATERIAL EXAMINED. TRAVIS COUNTY: Barton Springs. HAYS COUNTY: San Marcos Springs.

DIAGNOSIS. A small-sized species, averaging 1.13 mm in shell height, with broadly conical shell (Fig. 6H, I) and flaring aperture. Teleoconch surface punctate (Figs. 6I, 7C, 8E). Ctenidium absent, osphradium filling 19% of pallial cavity length (Fig. 13F). Central tooth of radula almost square-shaped, without basal cusps (Fig. 17A–D). Central and lateral teeth without enlarged central cusp (Fig. 17A–D). Style sac length 63% of stomach length; intestine with loop on style sac and complex coil in pallial roof (Fig. 13F). Ovary and testis fill about 30% of digestive gland length. Oviduct enters posterior end of albumen gland (Fig. 21C).

REMARKS. This species is distinguished by its broadly conical shell with punctate teleoconch sculpture, and unusual morphology of the central and lateral radular teeth.

DESCRIPTION. The shell is one and a third times as long as wide, and has four moderately rounded whorls. The protoconch and teleoconch surfaces are covered with a series of deep pits surrounded by slight elevations, with sculptural relief more pronounced in the teleoconch. Note that the teleoconch sculpture is sometimes arranged into spiral and/or collabral rows (Fig. 6I, 7C). The aperture is moderately thickened, pyriform above, rounded below, and flared except where the inner lip fuses with the penultimate whorl (6I). Umbilicus present.

Description of operculum and anatomy is based on study of material from San Marcos Springs. The flat operculum is one and a half times as long as wide, with the nucleus positioned at about 41% of the operculum length. Spiral growth lines are well developed on the operculum surface. The ventral surface lacks a process or thickening.

Note that the lateral angles of the central tooth of the radula project down, imparting an almost square-shape to the tooth (Fig. 17C). The central and lateral radula teeth have as many as 18 and 22 cusps, respectively. The basal process of the central tooth is somewhat thickened. The stomach has a small caecal appendix (Fig. 18C). The looping of the intestine onto the right side of the style sac is shown in Fig. 18C. The intestine coil in the pallial roof has an extra loop to the inside of the previous loop with the long axes of the loops oriented parallel to the pallial cavity length. Note that the coil closely resembles that of *P. imitata* (compare Fig. 13D and F).

The ovary and testis, both without lobes, fill 32% and 35% of the pallial cavity length. The seminal vesicle exits from the anterior end of the testis and is composed of several thickened loops posterior to the stomach (Fig. 18C). The anteriormost 60% of the prostate is pallial. The capsule gland is over twice as long as the albumen gland, lacks an anterior twist or bend, and has a terminal opening. The oviduct coil is considerably posterior to the end of the albumen gland. The bursa is heart-shaped, and the short duct exits from the end of the shorter axis. The seminal receptacle enters the left side of the oviduct coil. Note that the oviduct widens greatly as it merges with the albumen gland.

HOLOTYPE. ANSP 359092 (Fig. 6H).

PARATYPES. ANSP A10623G.

TYPE-LOCALITY. San Marcos Springs, Hays County (Fig. 1, Locality 3).

DISTRIBUTION. Edwards (Balcones Fault Zone) Aquifer in Hays and Travis Counties (Fig. 1, Localities 2, 3).

ETYMOLOGY. The epithet refers to the punctate teleoconch sculpture characteristic of this species.

Subfamily Littoridininae

Balconorbis Hershler & Longley, new genus

DIAGNOSIS. Shell (Fig. 23A, B, E–H) minute (width about 1.0 mm), planispiral, transparent, colorless. Protoconch and teleoconch sculpture consisting of spiral lines (Fig. 7G). Operculum paucispiral with sub-central nucleus. Animal unpigmented and without eyespots. Pallial cavity longer than wide, ctenidium absent, osphradium filling 24% of

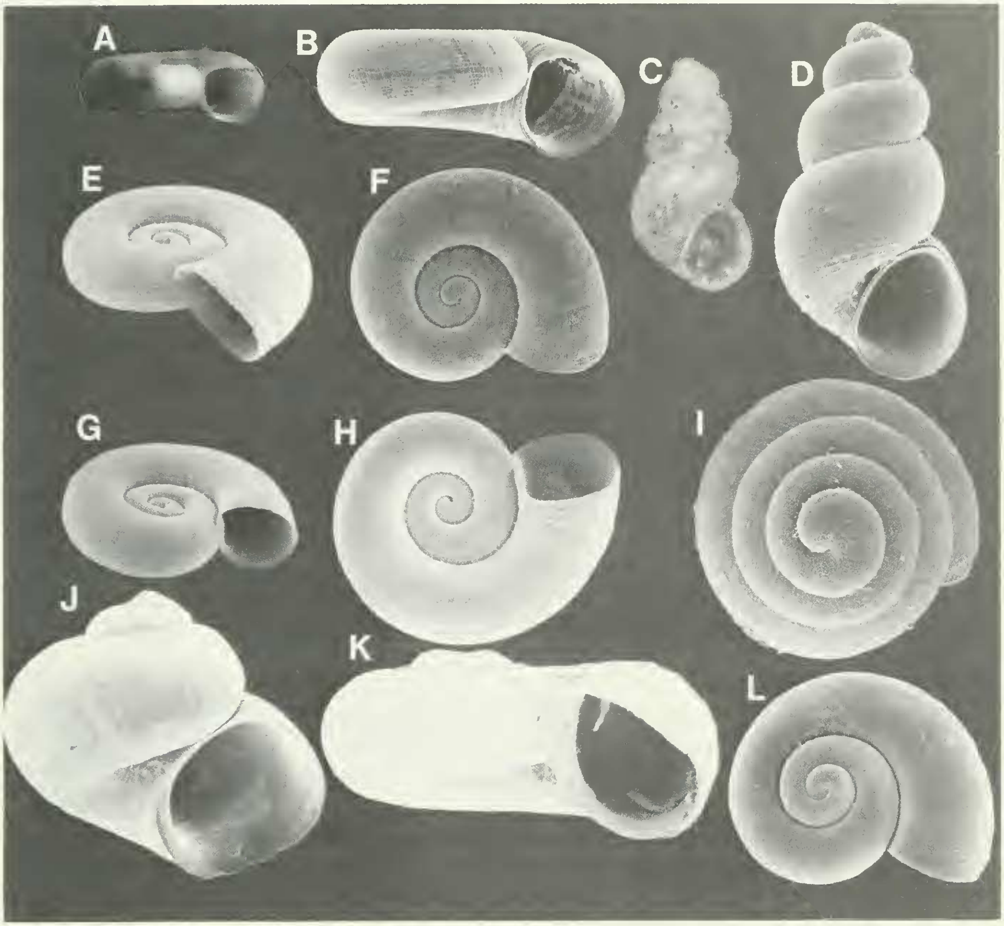

FIG. 23. Shells of *Balconorbis uvaldensis* (A, B, E–H; Locality 30), *Stygopyrgus bartonensis* (C, D, I; Locality 2), *Horatia klecakiana* (J), and "*Horatia*" sp. (K,L). Shell widths are as follows: A (1.02 mm, holotype), B (1.15 mm), C (shell height, 0.97 mm, holotype), D (shell height, 0.97 mm), E (0.932 mm), F (0.986 mm), G (0.803 mm), H (1.03 mm), I (0.513 mm), J (1.48 mm), K (1.6 mm), and L (1.83 mm).

pallial cavity length (Fig. 13H). Central tooth of radula (Fig. 17E–G) with single pair of basal cusps arising from lateral angles. Intestine with U-shaped loop in posterior portion of pallial roof; long axis of loop almost perpendicular to pallial cavity length (Fig. 13H). Anteriormost 47% of prostate pallial. Penis with single spherical lobe on outer curvature bearing a large apocrine gland (Fig. 24B). Capsule gland (Cg) with two tissue sections and terminal opening (Fig. 25B); posterior end of albumen gland coiled. Sperm pouches absent; sperm stored in anterior coil of oviduct. Spermathecal duct (Sd) issues from posterior end of pallial oviduct (where oviduct enters), joins capsule gland anteriorly.

REMARKS. The minute planispiral shell with spiral sculpture and absence of sperm pouches in the female reproductive system distinguish this genus from other littoridinines.

TYPE-SPECIES. *Balconorbis uvaldensis* Hershler & Longley, new species.

DISTRIBUTION. The Edwards (Balcones Fault Zone) Aquifer in Uvalde County.

ETYMOLOGY. The generic name is derived by combining Balcones, referring to the pres-

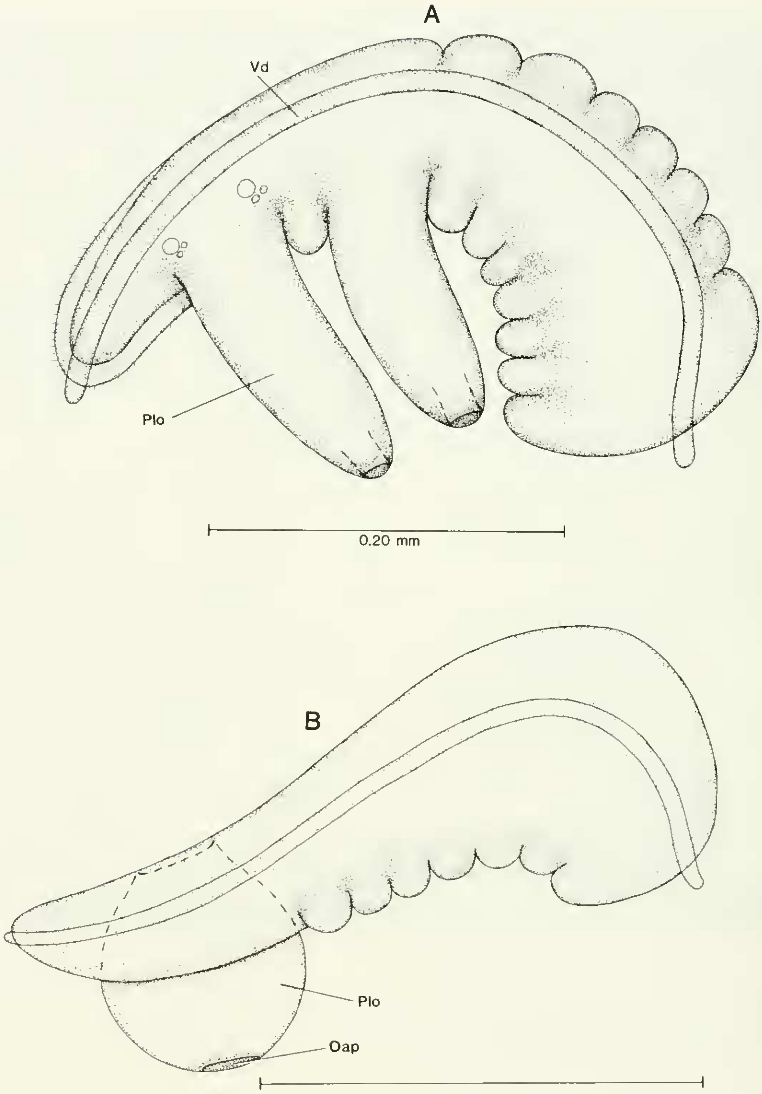

FIG. 24. Penes (dorsal aspect) of *Stygopyrgus bartonensis* (A) and *Balconorbis uvaldensis* (B). The dashed lines in the penial lobes (Plo) of *Stygopyrgus bartonensis* indicate the narrow distal ends of the ducts in the lobes. Note the lack of undulation of the vas deferens (Vd) in the penes. Both scale lines equal 0.20 mm. Oap = opening of apocrine gland; Plo = penial lobe; Vd = vas deferens.

ence of this genus in the Balcones Fault Zone region, with the Latin word *orbis*, referring to the circular outline of the shell.

Balconorbis uvaldensis Hershler & Longley, new species

Figs. 7G, 13H, 17E–G, 23A, B, E–H, 24B, 25B

MATERIAL EXAMINED. UVALDE COUNTY: King Farms Well; R. Carnes Well; R. K.

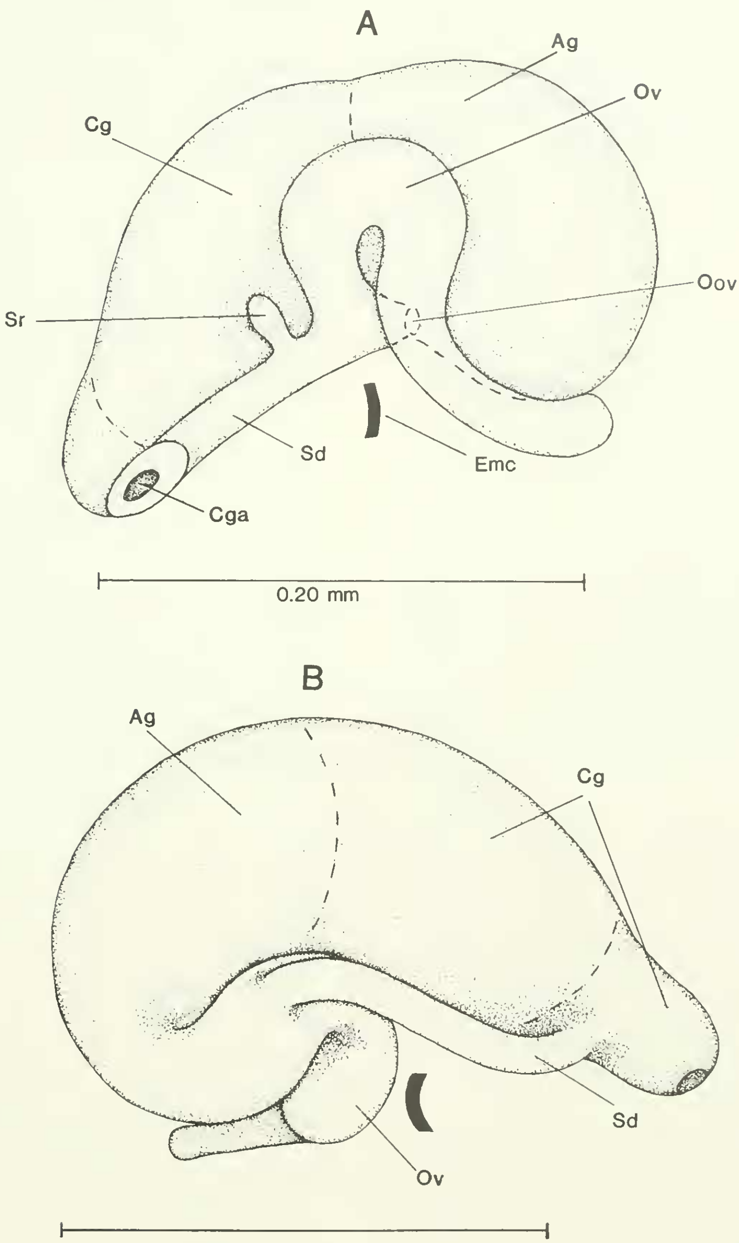

FIG. 25. Female reproductive morphology of *Stygopyrgus bartonensis* (A) and *Balconorbis uvaldensis* (B). The left aspect is shown in A and the right aspect in B. Note that both species lack a bursa copulatrix and have two tissue sections in the capsule gland (Cg), as indicated by dashed lines. Ag = albumen gland; Cg = capsule gland; Cga = capsule gland opening; Emc = posterior end of pallial cavity; Oov = opening of oviduct into pallial oviduct; Ov = oviduct; Sd = spermathecal duct; Sr = seminal receptacle.

Dunbar Well; S. Moerbe Well; G. Ligocky Well; Uvalde National Fish Hatchery Well.

DESCRIPTION. The shell has 2.75–3.0 tubular whorls and varies in width from 0.9 to 1.22 mm. Note that the spiral lines, which appear ragged on the protoconch (compared to the teleoconch lines), extend almost to the apex (Fig. 7G); and no other protoconch sculpture is present. The teleoconch also has numerous strong collabral growth lines which cross and often offset the spiral lines. The collabral lines are of highest relief near the aperture (Fig. 23G). The body whorl has about 50 spiral lines. The thin-lipped aperture is wider than long. The peristome is fairly straight while the rest of the lip is rounded.

The description of operculum and anatomy is based on study of specimens from G. Ligocky Well. The flat, thin operculum is wider than long, with about 2.5 whorls. The nucleus is positioned at 41% of the operculum length.

The central tooth of the radula is trapezoidal in shape with widely diverging lateral angles (Fig. 17E–G). Note that the cusps of the central teeth either come to a point (Fig. 17E, G) or are somewhat rounded (Fig. 17F). The anterior and posterior stomach chambers are well distinguished externally. The stomach lacks a caecal appendix. The anus, typically positioned near the mantle edge in hydrobiids, is about 30% back along the pallial cavity length (Fig. 13H).

The ovary and testis are without lobes. The vas deferens exits from the anterior end of the testis and consists of a few non-thickened coils posterior to the stomach. The penis is attached to and coils on the right side of the "neck", and is twice as long as the snout. Small folds extend for about two-thirds of the penis length from the base along the inner curvature. While attached to the right edge of the penis (about 0.08 mm from the tip), the penial lobe was folded under the penis (to the left side, as in Fig. 24B) in all but one specimen dissected. In that specimen the penial lobe simply projected to the right of the narrow attachment area. It is possible that the typical condition resulted from muscle contraction during fixation. The near-circular penial lobe measures about 0.10 mm across. The glandular opening is terminal and wide (Oap). The glandular lumen is fairly large and the gland is apocrine in type. The vas deferens does not coil in the penis.

The anterior end of the ovary abuts against the stomach. The coiled portion of the anterior oviduct has several swellings where sperm is presumably stored. Taking the coiled portion of the albumen gland into account, this gland is equal in length to the capsule gland. The anterior capsule gland section is about half the length of the posterior section and is clear, while the latter is white. Note the blunt anterior end of the capsule gland. The spermathecal duct (Sd) issues from the albumen gland just at the point where the former receives the oviduct. The spermathecal duct is largely ventral to the pallial oviduct and fairly thickened. It enters the capsule gland 0.04 mm from the terminal capsule gland opening.

HOLOTYPE. ANSP 359084 (Fig. 23A).

PARATYPES. ANSP 359085/A10623A.

TYPE-LOCALITY. G. Ligocky Well, Uvalde County (Fig. 1, Locality 30).

DISTRIBUTION. As for genus (Fig. 1, Localities 23, 27, 28, 29, 30, 31).

ETYMOLOGY. The epithet refers to the distribution of this species in Uvalde County.

Stygopyrgus Hershler & Longley, new genus

DIAGNOSIS. Shell (Fig. 23C, D, I) minute (about 1.0 mm in height), elongate-conic, transparent, colorless. Protoconch sculpture pitted (Fig. 23I); teleoconch sculpture consisting of spiral lines. Operculum paucispiral; nucleus positioned at 36% of operculum length. Pallial cavity about as wide as long, ctenidium absent, osphradium filling 25% of pallial cavity length (Fig. 13I). Central tooth of radula with one pair of basal cusps arising from prominent lateral angles. Intestine with U-shaped loop in pallial roof; long axis of loop perpendicular to pallial cavity length (Fig. 13I). Ovary and testis filling 33% and 60% of digestive gland length, with ovary covering posterior half of stomach. Half of prostate pallial; slender penis with two glandular lobes on inner curvature (Fig. 24A). Capsule gland with two tissue sections and subterminal, muscularized opening (Fig. 25A). Oviduct coil, spermathecal duct, and seminal receptacle appressed to left side of pallial oviduct; bursa absent. Oviduct and spermathecal duct open jointly into anterior end of albumen gland. Seminal receptacle opens into spermathecal duct; anterior end of spermathecal duct fused with capsule gland opening.

REMARKS. The minute, elongate-conical shell and unique configuration of the female reproductive system distinguish this genus from other Littoridininae.

TYPE-SPECIES. *Stygopyrgus bartonensis* Hershler & Longley, new species.

DISTRIBUTION. Thus far known only from Barton Springs, Travis County.

ETYMOLOGY. The generic name is derived from the Greek words *Stygos*, meaning lower world, and *pyrgos*, meaning tower, and refers to the phreatic habit and elongate shell of this taxon.

Stygopyrgus bartonensis Hershler & Longley, new species
Figs. 13I, 17H, I, 23C, D, I, 24A, 25A

MATERIAL EXAMINED: TRAVIS COUNTY: Barton Springs.

DESCRIPTION. The shell has 4.0–4.6 well-rounded whorls. Shell height varies from 0.97–1.3 mm. Note that the pitted microsculpture is best developed on the first half whorl of the protoconch (Fig. 23I). A total of about 20 fairly regularly spaced and pronounced spiral lines are found on the body whorl. Note that the lines are poorly developed to absent on the adapical third of the whorl. Collabral growth lines are also well developed on the teleoconch, although of lower relief than the spiral lines. The aperture is longer than wide, somewhat angled above, and touches the penultimate whorl. The lip is slightly thickened and does not flare. The umbilicus is chink-like.

The operculum is thin and flat. The central tooth of the radula is trapezoidal in shape, with diverging lateral angles (Fig. 17H, I). The dagger-like cusps of all four tooth types are elongate. The stomach lacks a caecal appendix. The anterior and posterior stomach chambers are well-distinguished externally.

Both gonads are without lobes. The seminal vesicle exits from the anterior end of the testis and consists of a few thickened coils posterior to the stomach. The penis is attached to and coils on the right side of the "neck," and is five times as long as the snout. The posterior half of the penis has deep folds (Fig. 24A). The two penial lobes, of similar appearance, are elongate (three times as long as wide), without folds, with a narrowed tip, and with a terminal pore through which glandular products are secreted. The glandular lumen is fairly large, filling about half to two-thirds of the penial lobe, and terminate distally in a narrow neck. The general appearance of the glandular lobe is similar to that described for *Mexipyrgus* Taylor, 1966 (Taylor, 1966; Hershler, 1985). A few glandular clusters are scattered throughout the penis and the penial folds have glandular edges. The small section of penis between the lobes and tip is lined (at the edges) with ciliated columnar epithelia. The vas deferens does not coil in the penis. Small spherical epibionts were seen clinging to the distal ends of the penial lobes.

The capsule gland is slightly larger than the albumen gland (Fig. 25A). The albumen gland is clear. The anterior section of the capsule gland narrows somewhat and is clear, while the much larger posterior section is yellow. The capsule gland opening is very slightly posterior to the anterior end of the gland. The U-shaped oviduct loop is centered at the junction between the albumen and capsule glands. The narrow posterior extension of the fused oviduct and spermathecal duct opens into the anterior end of the albumen gland on its left side. The seminal receptacle has a pink sheen and is less than 10% of the pallial oviduct length. Note that the seminal receptacle is positioned anterior to the end of the pallial cavity. The spermathecal duct joins the posterior side of the muscular capsule gland opening.

HOLOTYPE. ANSP 359093 (Fig. 23C).

PARATYPES. ANSP A10623H.

TYPE-LOCALITY. Barton ("Concession") Springs (Fig. 1, Locality 2).

DISTRIBUTION. As for genus.

ETYMOLOGY. The epithet refers to the type-locality.

DISCUSSION

Systematic relationships. A comparison among the nine species considered in this paper, as well as phreatic "*Orygoceras*" sp. (also known from south-central Texas), involving 40 binary-coded characters (72% from anatomy), is given in Appendix 4. A phenogram based on these data is shown in Fig. 26. As seen in the phenogram, the seven *Phreatodrobia* spp. form a cluster quite distinct from the remaining three species, all of which are monotypic littoridinines. The description of *Balconorbis* and *Stygopyrgus* brings the total of described phreatic littoridinine genera in the Western Hemisphere to four: *Paludiscala* and *Coahuilix* were previously described from (and considered en-

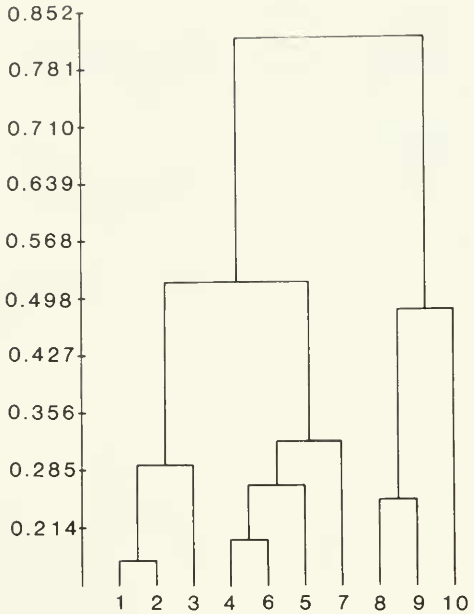

FIG. 26. Phenogram showing similarities among 10 species of phreatic Hydrobiidae from south-central Texas. The numbering of species is as in Appendix 4, which is also the source of the data used to generate the phenogram.

demic to) the Cuatro Ciénegas Basin in northern Mexico (Taylor, 1966; Hershler, 1984, 1985). A comparison among these taxa involving 16 morphological features is given in Table 5 and the anterior portion of their female reproductive systems is schematically diagrammed in Fig. 27. "*Orygoceras*" sp. is not included in this comparison as it has a number of unique character-states and probably represents an offshoot within the Littoridininae separate from the lineage(s) to which these other four genera belong to. The most similar pair among these four genera is *Paludiscala* and *Coahuilix*. Their penes are nearly identical as is the groundplan of their female reproductive systems, typified by the possession of a large-sized bursa, loss of the seminal receptacle (although a presumably secondarily-derived one is found in *Paludiscala*), and joint opening of the oviduct and sperm duct into the posterior section of the albumen gland (Fig. 27A, B). We believe that these two genera are closely related and belong to the same lineage within the Littoridininae.

The penis of *Balconorbis* is the same type as that of *Paludiscala* and *Coahuilix*, with a single spherical lobe on the outer curvature bearing an apocrine gland, and its female reproductive system (Fig. 27C) could represent a modification of that of the latter two genera involving loss of the bursa and resulting anterior extension of the sperm (now effectively a spermathecal) duct to join the capsule gland. Other character-states found in *Balconorbis*, notably the spiral protoconch microsculpture, could mitigate against a close phyletic relationship of this genus with those from Cuatro Ciénegas, although the value of this feature in separating higher taxa has recently been questioned (Hershler, 1985).

The mammiform penial glands and aspects of the female reproductive system (presence of a seminal receptacle and muscularized capsule gland opening, position of oviduct coil on left side of pallial oviduct) of *Stygopyrgus* readily distinguish this genus from the other three. *Stygopyrgus* may belong to a separate (from the above) littoridinine invasion of the phreatic habitat, perhaps from an ancestor belonging to the *Mexipyrgus-Durangonella* group (Hershler, 1984). Note that *Mexipyrgus* and *Durangonella* also have a muscularized anterior portion of the capsule gland and elongate, glandular (mammiform in *Mexipyrgus*) penial lobes. In conclusion, it appears that *Balconorbis* and *Stygopyrgus* may have close relatives among phreatic or epigean hydrobiids of the southwestern United States and northern Mexico.

Phreatodrobia nugax and *P. micra* were previously considered congeners of *Horatia s.s.* and *Hauffenia s.s.* from Europe. This is not an unrealistic possibility: such a situation exists for two Edwards Aquifer crustacean genera, *Monodella* Maguire and *Palaemonetes* Heller, both of which are considered to be of Tethyan origin and of brackish-water or marine ancestry (Stock, 1976; Strenth, 1976). The Hydrobiinae of Europe and North America also probably share a common, brackish-water ancestor (Johannson, 1956; G. M. Davis, 1979). A number of general similarities are seen between the above two sets of hydrobiid taxa. Note that *Horatia* and *Hauffenia* also have a low trochoid-planispiral shell (Binder, 1957, fig. 1; Pollonera, 1898, fig. 2); intestinal loop (simple) in the pallial roof (Boeters, 1974, fig. 3; Hershler, personal observations); bursa copulatrix positioned largely posterior to the albumen gland; oviduct coil located on the left

TABLE 5. Comparison of 16 morphological features among phreatic littoridinine genera of Texas and Mexico. Data regarding *Paludiscala* and *Coahuilix* are from Hershler (1985).

	Balconorbis	*Stygopyrgus*	*Paludiscala*	*Coahuilix*
1. Maximum shell size (height or width, mm)	1.22	1.30	2.60	1.37
2. Shell form	planispiral	elongate-conic	elongate-conic	planispiral
3. Protoconch sculpture	spiral lines	punctate	punctate	punctate
4. Teleoconch sculpture	spiral lines	spiral lines	collabral costae	absent
5. Ctenidium	absent	absent	present	present*
6. Intestine loop in pallial roof	present	present	absent	absent
7. Number of penial lobes	1	2	1	1
8. Position of penial lobe(s)	outer curvature of penis	inner	outer	outer
9. Penial gland type	apocrine	mammiform	apocrine	apocrine
10. Anterior oviduct coil	ventral to pallial oviduct	on left side of pallial oviduct	absent	present
11. Oviduct opens into	posterior tip of albumen gland	anterior end of albumen gland	posterior section of albumen gland	posterior section of albumen gland
12. Bursa copulatrix	absent	absent	present	present
13. Seminal receptacle	absent	present	present**	absent
14. Openings of spermathecal duct and capsule gland	fused	fused	fused	separate
15. Number of capsule gland tissue sections	2	2	3	2
16. Capsule gland opening	simple	muscularized	simple	muscularized

*Ctenidium absent in *C. hubbsi*, present in *C. landyei*.
**Seminal receptacle secondarily derived.

side of the pallial oviduct, and seminal receptacle opening into the oviduct coil (Radoman, 1966, fig. 8; Hershler, personal observations). Such general similarities also extend to the radula (see Fig. 27C, D for European genera) and protoconch microsculpture (Fig. 7I). The similarity of shell form, however, is superficial, the shell of the European genera (Fig. 23J) is larger, thicker, and more globose than that of any *Phreatodrobia*. Both *Horatia* and *Hauffenia* have penial lobes (Boeters, 1974, fig. 2; Giusti *et al.*, 1981, fig. 1), and the penial surface has complex glandular swellings (Hershler, personal observations), character-states not seen in any *Phreatodrobia*. No European hydrobiid has the thickened opercular process seen in the two *Phreatodrobia* spp. Other character-states seen in some *Phreatodrobia*, but not in any European hydrobiids, include a highly complex intestinal coil in the pallial roof, lack of basal cusps on the central tooth of the radula, and a coiled anterior end of the capsule gland. These differences suggest that *Phreatodrobia* represents a separate adaptive radiation meriting generic distinction from *Horatia*, *Hauffenia*, and other European hydrobiines.

Several other phreatic taxa are also known from North America, notably *Antrobia* Hubricht, *Fontigens* Pilsbry, *Antroselates* Hubricht, and "*Horatia*" (Hubricht, 1940). While none of these taxa has received detailed anatomical study, a limited comparison can be made with *Phreatodrobia*. *Fontigens*, while having a hydrobiine-type female reproductive system (Hershler, personal observations), is clearly separated from all other North American Hydrobiidae by its unique penis, which has two accessory glands fed by thickened ducts which run through the penis base to end blindly in the nuchal cavity. *Antroselates*, while lacking basal cusps on the central

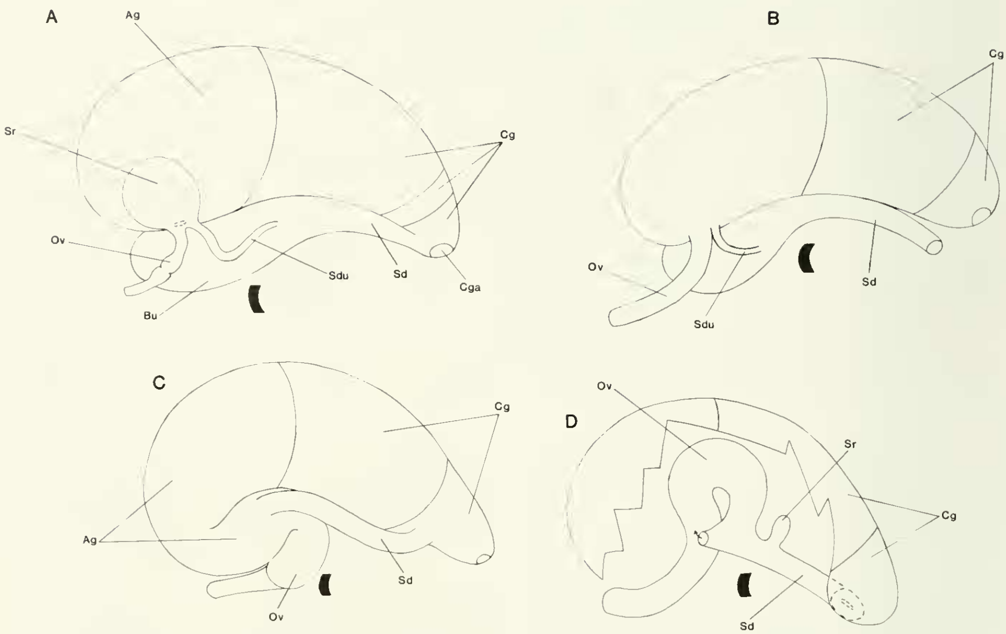

FIG. 27. Schematic representation of the female reproductive systems of *Paludiscala* (A), *Coahuilix* (B), *Balconorbis* (C), and *Stygopyrgus* (D). The right aspect is shown in all cases. In D, the arrow indicates the opening of the oviduct (Ov) into the pallial oviduct. Ag = albumen gland; Bu = bursa copulatrix; Cg = capsule gland; Cga = capsule gland opening; Ov = oviduct; Sd = spermathecal duct; Sdu = sperm duct; Sr = seminal receptacle.

tooth of the radula (Hubricht, 1963), as do some *Phreatodrobia*, is much larger (shell height, > 5 mm) and has an elongate, high-spired shell (Hubricht, 1963, pl. 8). "*Horatia*", collected from Manitou Cave in Alabama (Hubricht, 1940), has a near-planispiral shell (Figs. 23K, L) and an intestinal loop in the pallial roof (Hershler, personal observations), but differs from *Phreatodrobia* in having spiral lines on the protoconch (Fig. 7H). Note that the central teeth of the radula of both "*Horatia*" (Fig. 28A) and *Fontigens* (Fig. 28B) have short cusps, contrasting with the typically elongate cusps of *Phreatodrobia*. *Antrobia* has a hydrobiine female reproductive system, a slight intestinal loop in the pallial cavity, and a simple penis (Hubricht, 1971; Hershler, personal observations), yet differs from *Phreatodrobia* in having a thickened, globose, amnicolid-like shell (Hubricht, 1971, figs. 4–6) and spiral lines on the protoconch (Hershler, personal observations). On the basis of the limited data available, we conclude that while *Phreatodrobia* is probably not closely related to either *Fontingens* or *Antroselates*, it may belong to the same lineage as one or more of the remaining two taxa. It should also be pointed out that there are no known hydrobiines among epigean freshwater hydrobiids of North America.

As indicated in the phenogram, two pairs of *Phreatodrobia* spp. link closely: *P. micra* and *P. nugax* (0.175); and *P. conica* and *P. punctata* (0.200). *Phreatodrobia micra* and *P. nugax* share distinctive character-states that include presence of a ventral operculum process, an incomplete or complete ctenidium, and basal cusps on the central tooth of the radula. Note, however, that some populations of *P. nugax* have a smooth operculum. The shell similarity between these two species has been discussed above.

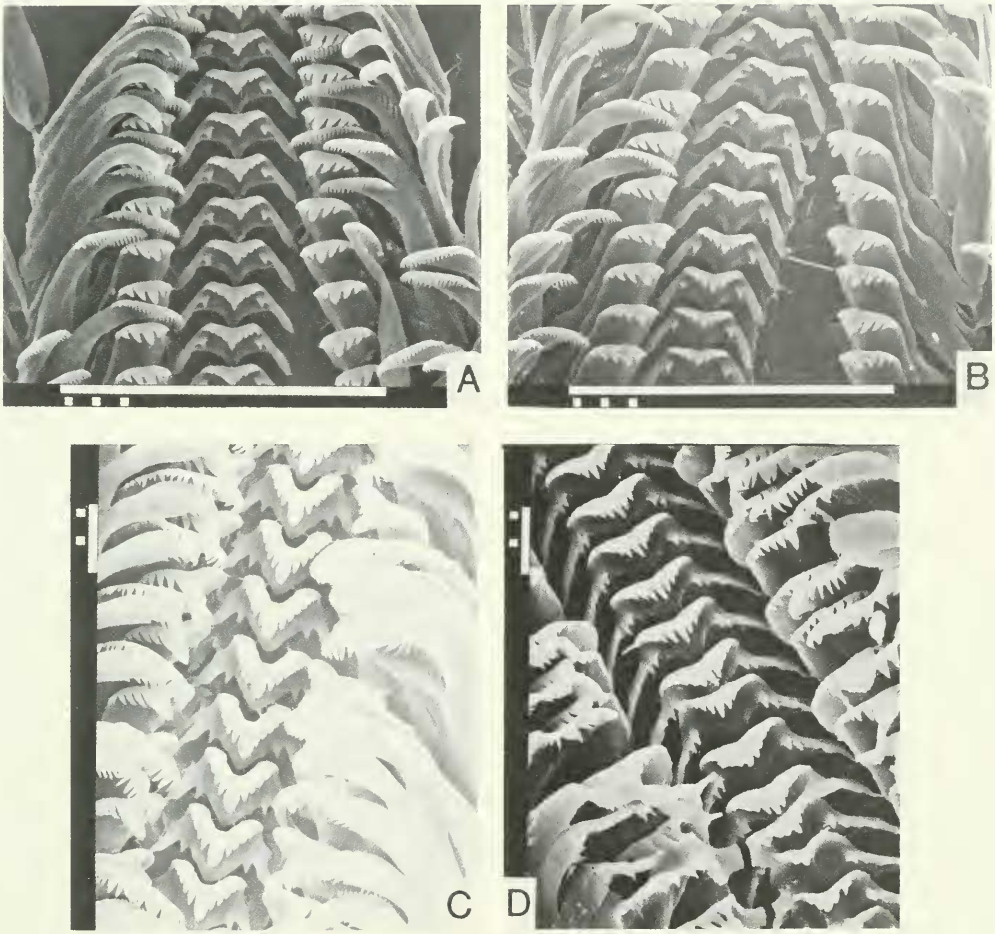

FIG. 28. Radulae of "*Horatia*" sp. (A), *Fontigens nickliniana* (B), *Horatia klecakiana* (C), and *Hauffenia subpiscinalis* (D). The scale bars in A and B equal 0.1 mm, while those in C and D equal 0.01 mm.

Phreatodrobia conica and *P. punctata* are distinguished from the above species pair by the following features: teleoconch sculpture consisting of low swellings or ridges; central tooth of radula square-shaped; lateral tooth of radula with numerous cusps; intestinal loop in pallial roof complex; and oviduct opening into posterior tip of albumen gland. The remaining three species, however, have a mosaic of character-states from the above two sets. *Phreatodrobia rotunda* has basal cusps on the central tooth of the radula, but has a complex pallial intestinal loop. *Phreatodrobia imitata* has a trapezoidal-shaped central tooth, but lacks basal cusps. The radula and pallial intestinal loop of *Phreatodrobia plana* are similar to those of *P. conica* and *P. punctata*, yet the organization of the bursa copulatrix complex in this species is near-identical to that of the other species pair.

Morphological diversity is marked within the genus, and a large number of unusual character-states are spread out among the various congeners. The morphological distinctiveness of the various species may explain the sympatry of five congeners in the aquifer beneath San Marcos Springs. Considering the mosaic pattern of character-state distribution among congeners, we feel that subgenera should not be recognized, although we suspect that *P. micra* and *P. nugax* are particularly closely related.

The problem of convergence. Several morphological features are probably particularly prone to convergence among phreatic hydrobiids. Blindness and lost body pigment are associated with invasion of the phreatic habitat (Culver, 1982) and have likely occurred in diverse hydrobiid lineages. Small body size, typical of phreatic hydrobiids, may also be associated with their purportedly food-poor environment (Culver, 1982). Several character-states are highly correlated with small body size, notably loss of the ctenidium, loss of sperm pouches, and looping of the intestine in the pallial roof. Again, shared possession of such character-states may not indicate phyletic affinity. If the systematist disregards all possible convergent character-states among these tiny snails, there may be rather few character-states from gross morphology remaining, as the anatomy of minute hydrobiids is rather simplified. Clarification of the systematic relationships of phreatic hydrobiids may only come when histological study of morphology is applied to the taxa in question. Not only does examination of tissue sections provide data on additional character-states, but it also can resolve whether given structures are homologous (a major concern when structures can be lost and regained), as convergence is unlikely to be precise at the cellular level. For examples of such studies applied to systematic relationships of rissoaceans, see Ponder (1984).

Distribution and habitat. The distribution of species (and subspecies) is shown in Fig. 29. Note that the fauna includes what may be locally endemic species as well as much more widespread species, a pattern also seen in the phreatic amphipod fauna of south-central Texas (Holsinger, 1967; Holsinger & Longley, 1980). While all species are found in the Edwards (Balcones Fault Zone) Aquifer, material collected from three localities in the drainage zone (Fig. 1, Localities 8–10) may not be from this aquifer. All three localities are wet caves, and all yielded only fresh shells. The source of water for the permanent streams in these caves is probably as follows: Natural Bridge Caverns (Glen Rose Formation), Honey Creek Cave (Cow Creek Formation), and Century Caverns (Lower Glen Rose Formation) (Knox, 1981; J. Knox, personal communication, 1984). Both the Glen Rose and Cow Creek are also Cretaceous limestone, but are members of the Trinity Group underlying the Edwards (Ashworth, 1983). While snail populations may not be living in the cave waters (the shells could have been washed in from elsewhere), it is still unlikely that the shells came from populations living in the Edwards (Balcones Fault Zone) Aquifer, given the sporadic occurrence of this aquifer in this region (Ashworth, 1983). It is therefore likely that the four species collected from these caves are found in aquifers other than the Edwards (Balcones Fault Zone). Note that Taylor (1974) collected living "*Horatia*" (possibly *P. micra* or *P. nugax*) from a spring in Real County, also in the drainage zone of the Edwards (Balcones Fault Zone) Aquifer. Also note that other invertebrate species (or sister species thereof) are found in the Edwards (Balcones Fault Zone) Aquifer as well as other aquifers in the Hill Country or Edwards Plateau (Mitchell & Reddell, 1971). All of the hydrobiid species may have considerably wider ranges than outlined above as the aquifers of south-central Texas have not been well sampled (see below).

The 14 artesian wells that yielded snails ranged in depth (beneath ground level) from 59–582 m (Table 2). All of these wells are tightly cased and there is no doubt that the snails were expelled from the deep artesian zone. Their habitat probably includes fractures, joints and caverns in the bedrock; and possibly, given the minute size of the snails, even interstices. Note, however, that snails were absent from eight wells in Bexar County (where three species occur), five of which yielded other troglobites (Table 2), a point which mitigates against common use of the interstitial habitat by the snails. It is likely that all or most of the species dwell in similar habitats in the recharge zone, where the aquifer is unconfined.

Faunal diversity in the Edwards (Balcones Fault Zone) Aquifer. The groundwater fauna of Texas has traditionally been sampled by collecting in wet caves. A tremendous effort has gone into such collecting and the aquatic fauna of caves in several physiographic regions of the state is well known (Mitchell & Reddell, 1971). Yet caves only offer a very small fraction of the total phreatic habitat. The deep artesian zone, for instance, is probably not accessible from caves. The recent application of sampling techniques involving plac-

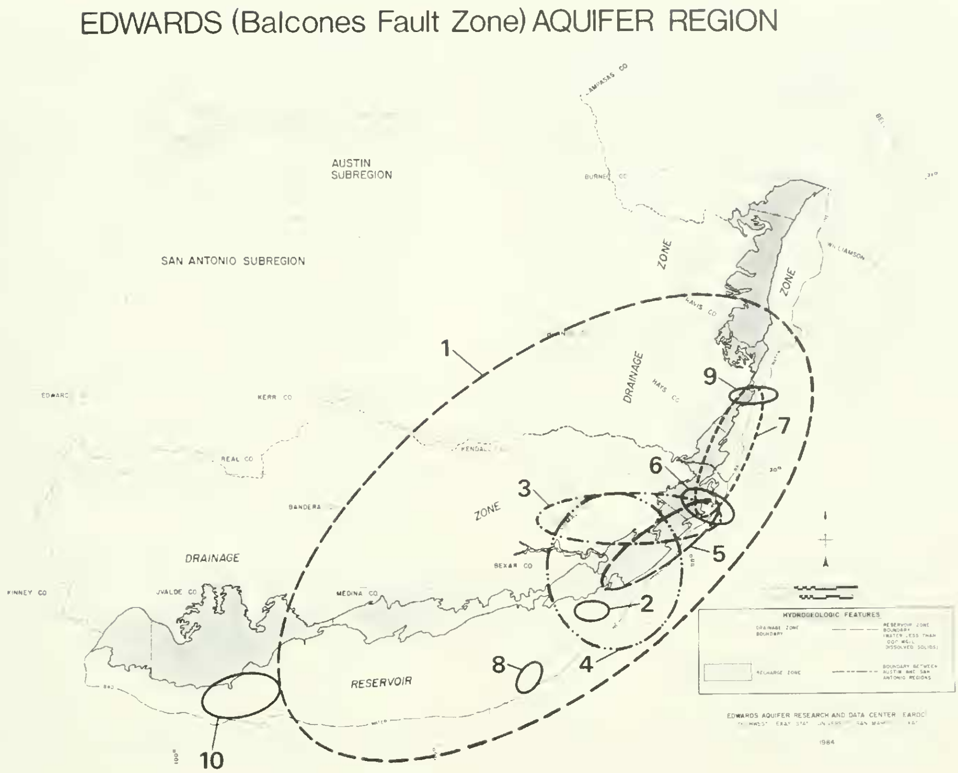

FIG. 29. Distribution of the 10 species and subspecies found in the Edwards (Balcones Fault Zone) Aquifer. 1 = *Phreatodrobia nugax nugax*; 2 = *P. n. inclinata*; 3 = *P. micra*; 4 = *P. conica*; 5 = *P. plana*; 6 = *P. rotunda*; 7 = *P. punctata*; 8 = *P. imitata*; 9 = *Stygopyrgus bartonensis*; 10 = *Balconorbis uvaldensis*.

ing nets over artesian well (for depths, see Table 2) or spring outlets has yielded many new species (see above) and demonstrated that a deep phreatic fauna does exist in some areas. Note that while the SWTSU Well (59 m deep) has yielded 20 troglobitic species, intensive collecting in the pool at the bottom of nearby Ezzell's Cave (in the same phreatic pool of the aquifer) only yielded nine species (J. D. Davis, 1979). With the description of the seven new species in this paper, the total described troglobitic fauna of the aquifer now totals 39 species. Collections from the localities considered in this paper have also yielded, apart from the snails, an additional 10–15 undescribed invertebrate species. Given the paucity of such sampling in most parts of the aquifer, a much larger number of species may yet await discovery. There is a large potential for discovery of additional new taxa in other aquifers of south-central Texas. The huge Edwards (Plateau) Aquifer, for instance, may contain a large number of sister taxa of the Edwards (Balcones Fault Zone) species, given that the two aquifers formed a single unit until at least the Miocene. Continued collecting in caves augmented by widespread application of the above sampling techniques will be necessary to more completely sample these and other aquifers in south-central Texas.

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APPENDIX 1. Data for all Texas localities considered in this paper. Numbers (in parentheses) refer to locations in Fig. 1. The collector and date(s) of collection are also given.

TRAVIS COUNTY: Salamander Cave (*1*), J. Reddell, 20 III 1966, 30°22′04″ N, 97°45′12″ W; Barton Springs (*2*), T. Spinelli, VI–VII 1982, R. Hershler, VI–VIII 1984, 30°16′ N, 97°47′ W.

HAYS COUNTY: San Marcos Springs (*3*), J. Davis, VIII–IX 1979, 29°54′ N, 97°56′ W; Artesian Well at Southwest Texas State University (*4*), G. Longley, IV–IX 1976, 29°53′24″ N, 97°56′08″ W.

COMAL COUNTY: Hueco Springs (A, B) (*5*), M. Brzozowski, VI–VII 1981, 29°46′ N, 98°08′ W; Guadalupe River drift (*6*), Pilsbry & Ferriss (1906), 29°45′30″ N, 98°08′30″ W; Comal Springs (main spring) (*7*), M. Brzozowski, VII–VIII 1981, 29°42′ N, 98°08′ W; Natural Bridge Caverns (River Styx at bottom of cave) (*8*), R. Hershler, 7 IX 1984, 29°41′22″ N, 98°20′30″ W; Honey Creek Cave (seeps feeding main spring from cave) (*9*), R. Hershler, 10 IX 1984, 29°50′ N, 98°30′ W.

KENDALL COUNTY: Century Caverns (stream at bottom of cave) (*10*), R. Hershler, 1 VIII 1984, 29°53′20″ N, 98°37′ W.

BEXAR COUNTY: Longhorn Portland Cement Co. Well (#2) (*11*), M. Brzozowski, II–IV 1981, 29°32′05″ N, 98°24 W; Brackenridge Zoo Well (*12*), City Water Board Artesian Station, Well 4 (*13*), M. Brzozowski, X 1980–VIII 1981, 29°25′48″ N, 98°26′14″ W; Union Stockyards Well (#3) (*14*), M. Brzozwski, 8–17 XIII 1980, 29°24′10″ N, 98°30′55″ W; City Water Board Mission Station Well (*15*), M. Brzozowski, 4–25 V 1981, 29°13′18″ N, 98°29′49″ W; J. H. Uptmore Well (#5) (*16*), M. Brzozowski, XII 1980–III 1981, 29°12′11″ N, 98°43′40″ W; Lackland City Water Co. Well (*17*), R. Rutland, VII–VIII 1979, 29°21′ N, 98°36′58″ W; City Public Service Board Well (#1) (*18*), R. Rutland, VII–IX 1979, 29°20′52″ N, 98°34′35″ W; Rio Vista Farms Well (*19*), M. Brzozowski, XII 1980–IV 1981, 29°20′23″ N, 98°44′38″ W; Verstraeten Brothers Well (*20*), H. Karnei, IV 1977–I 1978, 29°19′ N, 98°39′ W; O. R. Mitchell Well (*21*), H. Karnei, 14–23 VI 1977, R. C. Weidenfeld, 1–3 V 1980, 29°18′ N, 98°38′ W; J. W. Watts Well (*22*), M. Brzozowski, 5, 7 XI 1980, 29°17′38″ N, 98°41′20″ W.

UVALDE COUNTY: King Farms Well (*23*), M. Brzozowski, I–II 1981, 29°17′15″ N, 99°39′ W; D. C. Carnes Well (*24*), M. Brzozowski, I–II 1981, 29°16′37″ N, 99°40′51″ W; C. Reagan Well (*25*), M. Brzozowski, II– VIII 1981, 29°16′22″ N, 99°36′30″ W; W. C. Reagan Well (*26*), R. C. Weidenfeld, 1–25 III 1980, 29°16′06″ N, 99°34′ W; R. Carnes Well (*27*), M. Brzozowski, 2–16 II 1981, 29°13′59″ N, 99°51′52″ W; R. K. Dunbar Well (*28*), M. Brzozowski, 2–16 II 1981, 29°13′32″ N, 99°51′40″ W; S. Moerbe Well (*29*), M. Brzozowski, II–III 1981, 29°13′06″ N, 99°49′33″ W; G. Ligocky Well (*30*), R. C. Weidenfeld, I–VIII 1980, 29°11′37″ N, 99°48′38″ W; Uvalde National Fish Hatchery Well (*31*), R. C. Weidenfeld, I–IV 1980, 29°11′26″ N, 99°50′53″ W.

APPENDIX 2. Shell measurements. N = number of specimens, NW = number of whorls, PD = protoconch diameter, SH = shell height, SW = shell width, AH = aperture height, AW = aperture width, BW = height of body whorl. Locality numbers are those used in Fig. 1 and Appendix 1.

Species	Locality	N		NW	PD	SH	SW	AH	AW	BW
P. micra	6 (syntype)	1		2.5	—	0.419	1.02	0.419	0.434	0.419
	3	6	x̄	2.43	—	0.336	0.791	0.300	0.307	0.336
			s	0.103	—	0.023	0.050	0.020	0.015	0.023
	5(B)	14	x̄	2.49	—	0.471	1.08	0.416	0.454	0.454
	9	7	x̄	2.21	—	0.353	0.840	0.300	0.353	0.316
			s	0.19	—	0.037	0.092	0.036	0.040	0.065
	10	11	x̄	2.52	—	0.454	1.02	0.348	0.399	0.426
			s	0.048	—	0.039	0.088	0.036	0.046	0.032
P. nugax nugax	6 (holotype)	1		2.7	—	0.806	1.43	0.558	0.589	0.651
	1	1		2.7	0.317	0.837	1.05	0.372	0.434	0.651
	2	30	x̄	3.17	0.362	1.11	1.14	0.570	0.605	0.868
			s	0.22	0.015	0.12	0.07	0.044	0.04	0.083
	3	20	x̄	2.94	0.355	1.03	1.53	0.575	0.727	0.832
			s	0.11	0.025	0.13	0.12	0.068	0.058	0.097
	4	24	x̄	2.83	0.377	0.935	1.51	0.532	0.695	0.766
			s	0.17	0.022	0.10	0.13	0.07	0.057	0.07
	8	16	x̄	2.95	—	0.821	1.71	0.530	0.663	0.705
			s	0.17	—	0.094	0.108	0.040	0.039	0.075
	9	7	x̄	2.5	—	0.613	0.933	0.360	0.425	0.493
			s	0.058	—	0.059	0.066	0.03	0.039	0.052
	10	6	x̄	2.9	—	0.953	1.25	0.530	0.558	0.744
			s	0.2	—	0.13	0.20	0.059	0.068	0.098
	14	3	x̄	2.47	0.342	0.440	0.01	0.350	0.456	0.394
			s	0.06	0.011	0.041	0.026	0.023	0.023	0.012
	26	2	x̄	2.75	0.302	0.698	1.24	0.465	0.512	0.605
			s	—	0.007	0.022	—	—	0.022	0.066
P. nugax inclinata	11 (holotype)	1		3.4	0.376	1.18	1.33	0.496	0.620	0.899
	11	19	x̄	3.07	0.360	1.11	1.21	0.456	0.606	0.828
			s	0.17	0.017	0.092	0.11	0.059	0.057	0.079
P. rotunda	3 (holotype)	1		3.6	0.455	0.837	2.26	0.837	0.837	—
	3	9	x̄	3.42	0.392	0.769	2.01	0.769	0.741	—
			s	0.206	0.031	0.037	0.153	0.037	0.050	—
P. conica	5(B) (holotype)	1		3.75	0.36	1.61	1.21	0.744	0.729	1.22
	5(B)	5	x̄	3.82	0.343	1.76	1.41	0.831	0.778	1.27
			s	0.26	0.01	0.057	0.041	0.01	0.021	0.015
	5(A)	6	x̄	3.92	0.345	1.64	1.33	0.760	0.707	1.14
			s	0.12	0.01	0.061	0.057	0.015	0.021	0.037
P. plana	3 (holotype)	1		3.0	—	0.455	0.822	0.455	0.297	0.277
	3	8	x̄	2.93	—	0.450	0.820	0.444	0.305	0.273
			s	0.113	—	0.041	0.037	0.042	0.028	0.030
	7	1		2.75	—	0.376	0.752	0.356	0.257	0.277
P. punctata	3 (holotype)	1		3.8	0.297	1.05	0.791	0.512	0.434	0.744
	3	15	x̄	3.9	0.319	1.13	0.871	0.564	0.474	0.784
			s	0.15	0.015	0.081	0.055	0.050	0.035	0.056
P. imitata	20 (holotype)	1		3.5	0.36	1.07	0.81	0.43	0.47	0.713
	20	18	x̄	3.5	0.36	1.01	0.747	0.388	0.403	0.663
			s	0.12	0.01	0.038	0.42	0.26	0.27	0.040
	21	4	x̄	3.4	0.34	1.03	0.833	0.446	0.428	0.701
			s	0.12	0.026	0.020	0.08	0.034	0.03	0.015

APPENDIX 2 (Continued)

Species	Locality	N		NW	PD	SH	SW	AH	AW	BW
B. uvaldensis	30 (holotype)	1		2.75	—	0.434	1.02	0.31	0.372	0.326
	30	17	x̄	2.81	—	0.428	1.08	0.347	0.397	0.375
			s	0.12	—	0.044	0.088	0.035	0.029	0.036
S. bartonensis	2 (holotype)	1		4.0	—	0.970	0.495	0.337	0.287	0.594
	2	5	x̄	4.39	—	1.16	0.546	0.374	0.329	0.681
			s	0.26	—	0.11	0.023	0.015	0.021	0.050

APPENDIX 3A. Measurements of non-pallial organs and strucures. LST = stomach length, LSS = style sac length, LPO = pallial oviduct length, LBU = bursa length, LSR = seminal receptacle length, LOV = ovary length, LDG = digestive gland length, LPR = prostate length, LPP = pallial prostate length, LTS = testis length. Locality numbers refer to those used in Fig. 1 and Appendix 1.

Species (locality)		LST	LSS	LSS/LST	LPO	LBU	LSR	LOV	LOV/LDG	LPR	LPP	LPP/LPR	LTS	LTS/LDG
P. micra (3)	x̄	0.198	0.129	0.533	0.234	0.114	0.054	0.323	0.51	0.178	0.084	0.44	0.263	0.493
	s	—	0.01	0.057	0.052	0.01	0.021	0.448	0.12	—	0.007	—	0.69	0.14
	n	5	5	3	4	4	2	4	4	4	3	3	3	3
P. nugax (3)	x̄	0.370	0.200	0.564	0.455	0.23	0.095	0.97	0.67	0.44	0.198	0.52	0.574	053
	s	0.058	0.018	0.12	0.028	0.04	0.017	0.10	0.082	0.32	0.02	0.76	0.53	0.081
	n	6	5	5	4	4	5	5	6	4	3	3	4	4
P. rotunda (3)	x̄	0.430	0.277	0.7	0.461	0.188	0.079	0.489	0.22	0.396	0.238	0.60	0.436	0.21
	s	0.057	—	—	0.057	0.014	0.02	0.07	0.015	—	—	—	—	—
	n	3	1	1	3	2	3	3	3	1	1	1	1	1
P. conica (5B)	x̄	0.362	0.287	0.79	0.410	0.182	0.059	0.436	0.30	0.303	0.099	0.33	0.421	0.43
	s	0.042	0.034	0.09	0.057	0.015	—	0.073	0.11	0.025	0.016	0.07	0.86	0.014
	n	4	4	3	3	3	2	5	3	4	4	4	6	2
P. plana (3)	x̄	0.193	0.087	0.45	0.191	0.099	0.059	0.303	0.52	0.173	0.79	0.465	0.292	0.59
	s	0.01	0.01	0.058	0.01	—	—	0.061	0.11	0.03	—	0.07	0.025	0.75
	n	4	4	4	6	4	2	3	3	4	4	4	4	4
P. imitata (20)	x̄	0.23	0.18	0.67	0.246	0.16	0.04	0.213	0.342	0.28	0.125	0.45	0.28	0.405
	s	0.03	0.03	0.16	0.037	0.016	—	0.075	0.115	0.02	0.023	0.06	0.02	0.04
	n	6	6	6	8	4	4	5	5	3	3	2	3	2
P. punctata (3)	x̄	0.244	0.152	0.63	0.228	0.109	0.059	0.323	0.353	0.20	0.12	0.6	0.317	0.432
	s	0.03	0.011	0.12	0.011	0.042	—	0.037	0.049	—	—	—	0.034	0.01
	n	3	3	3	4	2	2	4	4	1	1	1	3	3
S. bartonensis (2)	x̄	0.193	0.191	0.80	0.311	—	0.030	0.261	0.334	0.139	0.069	0.50	0.426	
	s	0.019	0.03	0.067	0.05	—	0.014	0.077	0.091	—	—	—	0.13	0.14
	n	4	4	4	3		3	5	5	1	1	1	2	2
B. uvaldensis (30)	x̄	0.246	0.194	0.792	0.323	—	—	0.416	0.405	0.198	0.093	0.472	0.594	0.526
	s	0.041	0.029	0.048	0.02	—	—	0.054	0.037	0.024	0.01	0.051	0.139	0.083
	n	5	5	5	6	—	—	4	4	5	4	4	5	5

APPENDIX 3B. Measurements of pallial structures. LPC = pallial cavity length, LIC = intestine coil length, WIC = intestine coil width, LOS = osphradium length, LCT = ctenidium length, WCT = ctenidium width, NF = number of gill filaments, IMA = distance from anus to mantle edge. Locality numbers refer to those used in Fig. 1 and Appendix 1.

Species (locality)		LPC	LIC	WIC	LOS	LCT	WCT	NF	IMA	LIC/LPC	LOS/LPC
P. micra (3)	x̄	0.366	0.099	0.178	0.139	—	—	—	0.064	0.273	0.385
	s	0.057	0.014	0.028	—	—	—	—	0.019	0.033	0.064
	n	4	6	6	5	—	—	—	4	5	5
P.n. inclinata (11)	x̄	0.713	0.232	0.376	0.181	0.505	—	13.7	0.178	0.340	0.274
	s	0.054	0.07	0.056	0.031	0.014	—	1.42	—	0.13	0.037
	n	5	3	2	7	2	—	11	1	3	4
P.n. nugax (3)	x̄	0.754	0.289	0.319	0.183	0.578	0.119	14.4	0.178	0.40	0.25
	s	0.10	0.034	0.069	0.026	0.062	0.034	1.69	0.014	0.07	0.04
	n	13	7	7	12	9	5	11	5	7	12
(4)	x̄	0.792	0.218	0.356	0.174	0.590	0.178	13.0	0.198	0.31	0.222
	s	0.118	0.028	0.084	0.022	0.392	—	0.71	—	0.042	0.036
	n	5	2	2	5	4	1	5	1	2	5
(2)	x̄	0.729	0.396	—	0.158	0.560	—	12.4	0.139	0.54	0.235
	s	0.088	—	—	0.047	0.073	—	1.36	0.057	—	0.07
	n	5	1	—	5	5	—	11	4	1	2
(14)	x̄	0.382	0.139	0.198	0.153	0.322	0.079	11.0	0.109	0.32	0.41
	s	0.001	0.023	—	0.01	0.041	—	0.82	0.014	—	0.056
	n	3	3	1	4	3	1	4	2	1	4
(12)	x̄	0.455	0.265	0.257	0.119	—	—	8.5	0.119	0.44	0.26
	s	—	—	—	—	—	—	0.071	—	—	—
	n	1	1	1	1	—	—	2	1	1	1
(25)	x̄	0.653	0.168	0.244	0.191	0.614	—	9.0	0.158	0.247	0.28
	s	0.052	0.026	0.01	0.03	0.028	—	—	0.028	0.032	0.014
	n	3	4	4	3	3	—	1	3	3	2
P. rotunda (3)	x̄	1.08	0.644	0.337	0.139	—	—	—	0.119	0.64	0.13
	s	0.06	0.042	0.052	0.02	—	—	—	0.032	0.04	0.01
	n	5	2	3	3	—	—	—	5	2	3
P. conica (5B)	x̄	1.09	0.590	0.402	0.224	—	—	—	0.119	0.50	0.20
	s	0.073	0.082	0.042	0.063	—	—	—	0.028	0.07	0.05
	n	4	4	3	4	—	—	—	3	3	3
P. plana (3)	x̄	0.392	0.153	0.149	0.135	—	—	—	0.099	0.415	0.33
	s	0.063	0.03	0.017	0.025	—	—	—	—	0.15	0.059
	n	6	7	6	5	—	—	—	3	4	4
P. imitata (20)	x̄	0.600	0.33	0.247	0.155	—	—	—	0.125	0.36	0.26
	s	0.01	0.057	0.027	0.015	—	—	—	0.03	0.07	0.02
	n	6	6	6	6	—	—	—	3	4	6
P. punctata (3)	x̄	0.709	0.360	0.236	0.134	—	—	—	0.141	0.475	0.185
	s	0.068	0.03	0.053	0.01	—	—	—	0.012	0.02	0.017
	n	6	5	7	4	—	—	—	4	4	4
S. bartonensis (2)	x̄	0.302	0.094	0.198	0.089	—	—	—	0.079	0.270	0.246
	s	0.043	0.03	0.039	0.01	—	—	—	0.052	0.13	0.018
	n	5	4	5	5	—	—	—	3	4	5
B. uvaldensis (30)	x̄	0.671	0.172	0.232	0.160	—	—	—	0.210	0.26	0.24
	s	0.103	0.054	0.032	0.022	—	—	—	0.06	0.095	0.029
	n	8	6	6	8	—	—	—	5	6	8

APPENDIX 4. Comparison of 10 spp. of phreatic hydrobiids from south-central Texas involving 40 characters. OTU 1 = *Phreatodrobia micra*, 2 = *P. nugax*, 3 = *P. rotunda*, 4 = *P. conica*, 5 = *P. plana*, 6 = *P. punctata*, 7 = *P. imitata*, 8 = *Balconorbis uvaldensis*, 9 = *Stygopyrgus bartonensis*, 10 = *"Orygoceras"* sp. Data for *"Orygoceras"* sp. are from Hershler & Longley (in press).

	OTU									
Character	1	2	3	4	5	6	7	8	9	10
1. Maximum shell dimension >1.25 mm (0,1)	0	1	1	1	0	0	0	0	1	1
2. Shell form planispiral (0,1)	1	1	1	0	1	0	0	1	0	0
3. Shell form trochoid-low conic (0,1)	0	1	0	1	0	1	0	0	0	0
4. Shell form elongate-conic (0,1)	0	0	0	0	0	0	1	0	1	0
5. Shell uncoiled (0,1)	0	0	0	0	0	0	0	0	0	1
6. Protoconch microsculpture: spiral lines (0); punctate (1)	1	1	1	1	1	1	1	0	1	1
7. Teleoconch typically with spiral lines (0,1)	0	0	0	0	0	0	0	1	1	0
8. Teleoconch typically with irregular ridges (0,1)	0	0	0	1	1	1	0	0	0	0
9. Teleoconch typically with collabral costae and spiral threads (0,1)	0	0	0	0	0	0	1	0	0	0
10. Operculum concentric (0,1)	0	0	0	0	0	0	0	0	0	1
11. Operculum with ventral process (0,1)	1	1	0	0	0	0	0	0	0	1
12. Ctenidium (or vestige) present (0,1)	1	1	0	0	0	0	0	0	0	0
13. L osphradium/L pallial cavity typically >30% (0,1)	1	0	0	0	1	0	0	0	0	2
14. Number of intestinal loops in pallial cavity: 1 (0); 2 (1)	0	0	0	0	1	1	1	0	0	0
15. Long axis of loop(s): parallel to L pallial cavity (0); perpendicular (1)	1	1	0	1	0	0	0	1	1	1
16. Central radular tooth with basal cusps (0,1)	1	1	1	0	0	0	0	1	1	1
17. Central tooth shape: trapezoidal (0); square (1)	0	0	0	1	0	1	0	0	0	0
18. Lateral tooth with >20 cusps (0,1)	0	0	0	1	1	1	0	0	0	0
19. L style sac/L stomach >50% (0,1)	1	1	1	1	0	1	1	1	1	1
20. Intestine with loop on right side of style sac (0,1)	0	0	1	0	0	1	0	0	0	1
21. Pallial gonoducts more than four times as long as wide (0,1)	0	0	0	0	0	0	0	0	0	1
22. Penis lobed (0,1)	0	0	0	0	0	0	0	1	1	0
23. Penis with specialized glands (0,1)	0	0	0	0	0	0	0	1	1	0
24. L testis/L digestive gland >40% (0,1)	1	1	0	1	1	1	1	1	1	1
25. Seminal vesicle exits from anterior tip of testis (0,1)	1	0	1	1	1	1	1	1	1	1
26. Seminal vesicle coils on stomach (0,1)	1	0	0	0	1	0	0	0	0	0
27. L pallial prostate/L prostate >40% (0,1)	1	1	1	0	1	1	1	1	1	1
28. Vas deferens exits from prostate tip (0,1)	0	0	0	0	0	0	0	0	0	1
29. L ovary/L digestive gland typically >40% (0,1)	0	1	1	1	0	0	0	0	1	1
30. Sperm travels in female via: spermathecal duct (0); ventral gutter (1)	1	1	1	1	1	1	1	0	0	0
31. Capsule gland more than twice the length of albumen gland (0,1)	0	0	1	1	1	1	0	0	0	0
32. Anterior end of capsule gland typically coiled (0,1)	0	1	0	0	0	0	0	0	0	0
33. Capsule gland opening muscularized (0,1)	0	0	0	0	0	0	1	0	1	0
34. Capsule gland with >1 tissue section (0,1)	0	0	0	0	0	0	0	1	1	1

APPENDIX 4 (Continued)

Character	OTU									
	1	2	3	4	5	6	7	8	9	10
35. Posterior end of albumen gland coiled (0,1)	0	0	0	0	0	0	0	1	0	1
36. Albumen gland sac-like (0,1)	0	0	0	0	0	0	0	0	0	1
37. Oviduct coil positioned: on left side of albumen gland (0); posterior or ventral to gland (1)	0	0	1	0	0	1	0	1	0	0
38. Oviduct opens into posterior end of albumen gland (0,1)	0	0	0	0	0	1	1	1	0	1
39. Bursa present (0,1)	1	1	1	1	1	1	1	0	0	1
40. Seminal receptacle present (0,1)	1	1	1	1	1	1	1	0	1	0

Revised Ms. accepted 1 May 1985.